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*Mammals*

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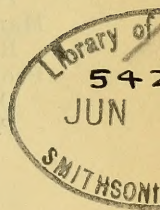
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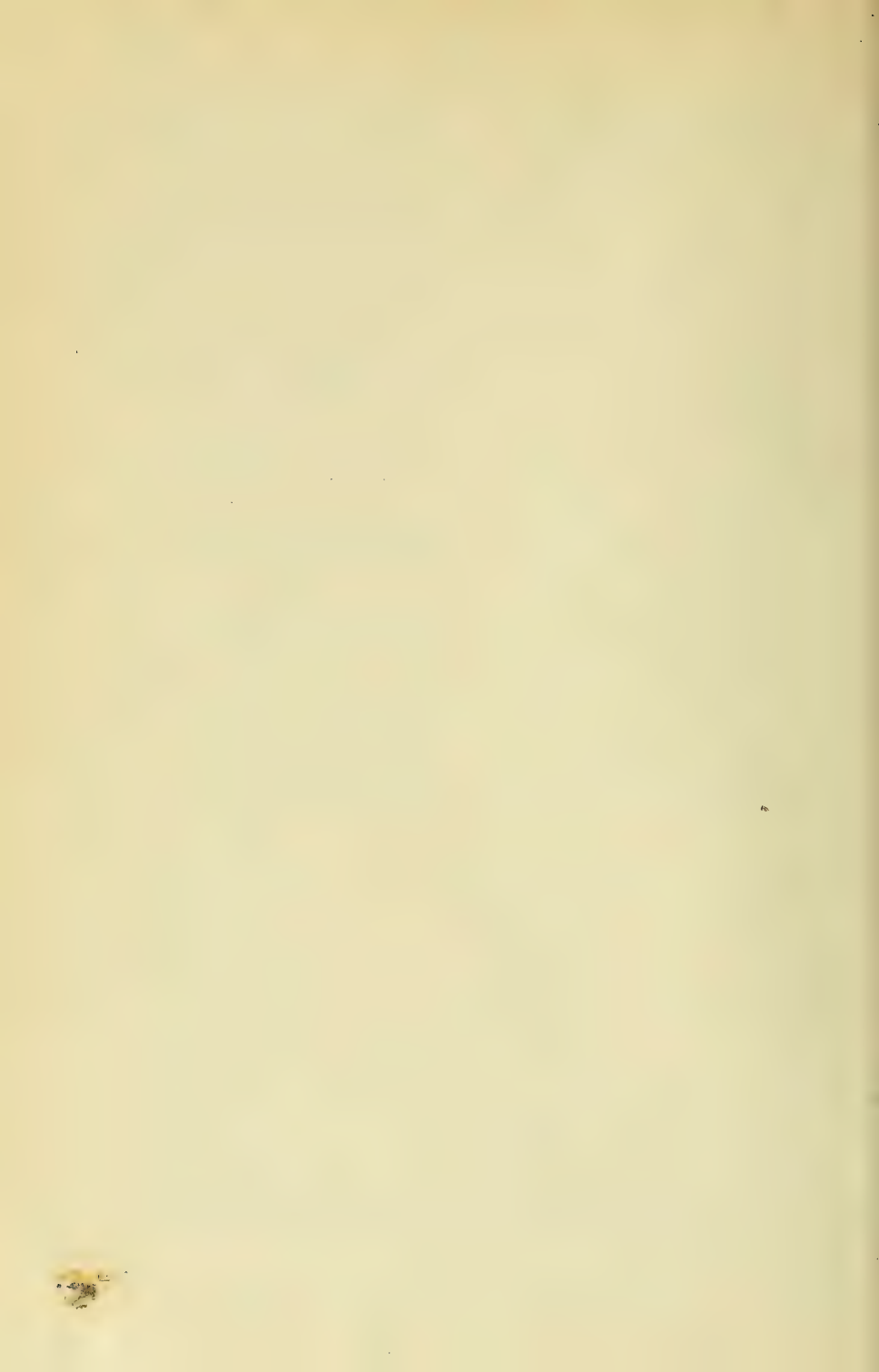
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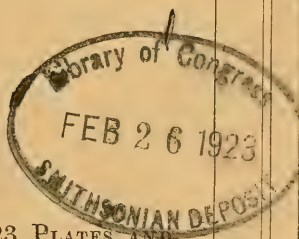
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TESTUDO LOVERIDGII BLGR.  
( $\frac{2}{3}$  natural size)





TESTUDO LOVERIDGII BLGR. ♀  
( $\frac{3}{4}$  natural size)







TESTUDO LOVERIDGII BLGR. ♂  
( $\frac{3}{4}$  natural size)

# PROCEEDINGS

OF THE

## GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

## ZOOLOGICAL SOCIETY OF LONDON.

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### PAPERS.

26. A Study of the Remarkable Tortoise, *Testudo loveridgii* Blgr., and the Morphogeny of the Chelonian Carapace.  
By JOAN B. PROCTER, F.Z.S.

[Received May 22, 1922 : Read June 13, 1922.]

(Plates I.-III.\*; Text-figures 1-21; and Table.)

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### INTRODUCTION.

In the preparation of the present paper, I am indebted to many persons for help and various courtesies. My especial thanks are due to Mr. A. Loveridge, for his generosity in allowing

\* For explanation of the Plates, see p. 526.

me to use the whole of his valuable collection for dissection and general study. Also to Sir John Bland-Sutton, for his gift of X-ray plates of the types and young, and facility to study the tortoises themselves beneath the fluorescent screen at Middlesex Hospital at a time when no specimens could be spared for dissection; and also to Mr. R. H. Burne, of the Royal College of Surgeons, for investigating the structure of the denticulated jaw, and the ribs, and for making slides of them.

The purport of the present work is to furnish a detailed description of this extraordinary Soft Tortoise, based upon the large series of specimens which have passed through my hands; especially of the peculiarly interesting structure of the bony carapace and its development, compared with cases of fenestration in *Testudo* and other groups. The recently discovered young is also described in comparison with the adult, and various notes on the habits of living specimens by Mr. Loveridge are appended.

#### GENERAL ACCOUNT.

##### *Material and history.*

In 1920, when Mr. G. A. Boulenger first examined this tortoise, then new to science, there were no specimens available for the making of a skeleton. The carapace, which feels soft and springy, was examined by cutting a flap in the abdominal shields, removing the viscera, and holding the animal against the light. When this is done, no bony matter of any kind can be detected; the carapace is seemingly translucent without ribs or costal plates: it was therefore described as boneless. The view obtained in this way is deceptive, as it is limited to the region of the second and third costal and vertebral shields on account of the restrictions of the fenestra in the plastron through which it is viewed; the shadows of the reduced costal plates, which are there, are entirely obscured by the black markings in the epidermal shields.

The young specimen described in his note\*, although agreeing in almost every particular with the type, excepting its convexity, was an anomalous specimen, not the young of *loveridgii*. In 1921, Mr. Loveridge sent a Kaffir on an expedition to hunt for further material, and the true young was found in the type-locality. This has a depressed carapace, but does not resemble the adult in general appearance. Since then further expeditions have succeeded in capturing more specimens, both adult, young, and half-grown, so that at one time and another I have been able to examine twenty-three spirit specimens, besides two specimens at present living in the Zoological Gardens. It has also been possible to prepare skeletons both of adult and young, and to make dissections.

After examining this new material, Mr. Boulenger agrees

\* Boulenger, C. R. Acad. Sci., Paris, t. 170, p. 264 (1920).

with me in my three principal amendments to his original description:—

1. That the type-specimens are fully adult.
2. That the adults have bony neural and costal plates present to a certain degree.
3. That the young has a more or less depressed carapace.

#### *Characteristics.*

*Testudo loveridgii* is already well known as the Soft-shelled Tortoise with the flat carapace, both these characteristics being entirely foreign to *Testudo* as previously defined.

In general appearance it looks as if it had been crushed in youth and had only survived by a miracle. When taken in the hand alive it has a boneless feeling which is uncanny; both carapace and plastron react to pressure on the abdominal region with a springy motion, and the animal is able to inflate itself to a slight degree.

Mr. Boulenger pointed out in his note that in the case of the plastron this softness is due to an enormous diamond-shaped fenestra, usually met with in the newly-hatched or very young of other species. The viscera thus exposed are protected by extremely thick, soft, dermis of a very tough nature.

The true structure of the carapace was revealed by X-rays quite accidentally, my original object being to compare the supposedly boneless adult with the young, in which the ribs show normal development. When viewed through the fluorescent screen, the adults presented an extraordinary appearance, the ribless vertebræ and more or less normal limb-girdles being overlaid by a bony network, intimately correlated with the net of sutures between the epidermal shields, and formed by the partial development of the neural and costal plates which had been apparently wanting, and which in other species compose the solid bony carapace (*vide* Pls. II. & III.). The significance of this bony network only became clear after considerable study of the X-ray plate taken at the time. The skeleton subsequently prepared corroborated every detail revealed in this plate, and also showed that the vertebræ are very remarkable in form. The animal is further remarkable in possessing what appear to be teeth, acrodont in type and similar to those met with in Agamoid lizards. Their regularity renders them quite unlike the serrations met with in some tortoises. The horny sheaths of the alveolar ridges are similarly denticulated.

In the detailed description which follows, these structures will be dealt with at greater length.

The species is still in a state of great instability, for apart from the immense range of variation to which it is subject, many abnormalities occur, such as the presence of horny shields proper to the more primitive Chelonians.

*Affinities.*

*Testudo loveridgii* is undoubtedly closely related to *T. tornieri* Sieb. Even before the skeletal characters were known, when the former was thought to be without a bony carapace, it was recognized as being nearer to the latter species than to any other; in fact, Mr. Loveridge took his first specimens to be *tornieri*. Comparison of their skeletons show that they are similar in structure.

Briefly, they are probably both derived from the *geometrica* group, *loveridgii* being one step further removed than *tornieri*.

*T. tornieri* differs from *T. loveridgii* in that the carapace is not quite so depressed. The bony plates beneath are rather more developed, and slightly different in arrangement. It has a ninth pair of well-developed costal plates, and the whole animal is relatively much longer, being about half as broad as long instead of two-thirds.

The supracaudal shield is also entire, instead of divided as is usually the case in *loveridgii*. It possesses, however, all the special peculiarities of *loveridgii*, including the deficient ribs, and fenestrated carapace and plastron, which produces a soft-shelled condition. It also appears, from its photographs, to have both jaws regularly denticulated.

Siebenrock's two specimens from Bussisi and Lindi are described as having soft shells, but he considered the condition of the carapace which he dissected away in one individual to be pathological (1904). The finding of a third specimen by Lönnberg at Njoro (1911) and the recent discovery of *loveridgii*, however, prove that it is merely physiological.

*Habitat and habits.*

*T. loveridgii* is found in the arid rocky country round Dodomo and Tabora in Tanganyika Territory. Its distribution seems to be restricted to rocky kopjes where great boulders of grey granite are scattered; the characteristic vegetation is of the thorn-bush type; capers are also numerous.

The tortoise is good at climbing up the face of the rock, and turns over easily after falling on its back. It can only be dislodged from crevices with difficulty, as it is able to inflate itself to a certain degree, and thus wedge itself firmly, using its legs as struts. It is also able to squeeze itself beneath stones, on account of the springy structure of its carapace.

It is probable that it lays a single oval egg (about 35 mm. long and 23 mm. in diameter), as such a one was recently dug up by Mr. Loveridge in the enclosure in which several females were penned. The embryo extracted from this egg is almost at the point of hatching, and I have little doubt that it is *loveridgii*; but it is not possible to be certain, as females of *T. pardalis* and *Cinixys belliana* were also in the pen, and tortoise-embryos are very similar to one another, and at this stage the more striking characteristics of *loveridgii* are not manifest.



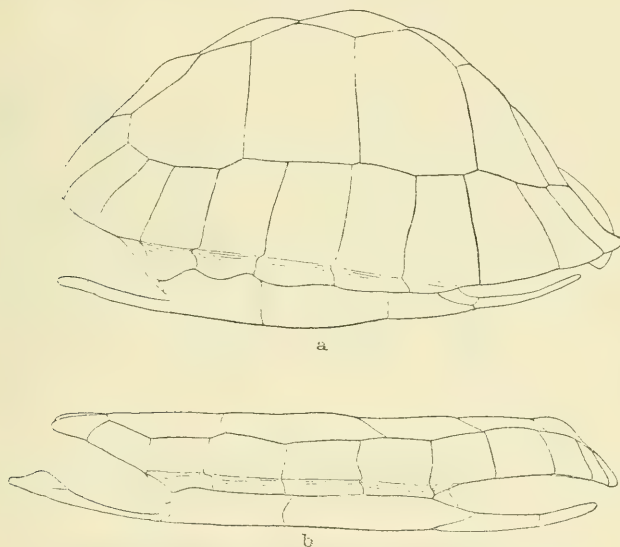
Further particulars as to habits will be found in the notes by Mr. Loveridge appended to this paper.

#### EXTERNAL CHARACTERS.

##### *Shape and proportions.*

The carapace of the adult is from three-quarters to four-fifths broad as long (actually 71 to 83 per cent.), excessively depressed, either flat or concave in the vertebral region; depth usually about one-fifth of the length. In text-fig. 1 (*q. v.*) the depressed carapace of *loveridgii* is compared with that of the normal *ibera*. Marginal region turning downwards and outwards abruptly, excepting the anterior border, which remains flat; marginals four to eight sometimes perpendicular. Sides straight, either

Text-figure 1.



Carapace of a normal Tortoise, *T. ibera* (a), compared with that of *T. loveridgii* (b).

parallel or oblique; anterior edge of shell straight or forming a slightly inverted curve, feebly serrated; posterior border rounded or obtusely pointed, also slightly serrated. Sometimes the greatest width is in the pectoral and sometimes in the pelvic region, but in the majority it is equal at and between these two positions. This depends upon the oblique or parallel trend of the sides of the carapace. In the table of measurements the breadth is always taken at mid-carapace.

The young are as broad as long and about one-third deep as long, and the carapace is uniformly convex and cordiform in outline. With growth these proportions change, the tortoise becoming narrower and more depressed. In order to show the precise nature of this change in form, the specimens in the appended table are graded according to age; the regular fall of the percentage values for breadth and depth are thus obvious, and could be well expressed by graphs.

In both adults and young the dimension of depth does not properly apply to the carapace *s. str.*, but to the thickness of the entire animal.

The plastron is large and projects beyond the carapace in front and falls short of it behind; fore-lobe truncate, hind-lobe deeply cleft, the two about equal in length and nicely shaped around the limbs; bridge very variable in width, usually about once and a half the length of either lobe. In the young the breadth of the entire plastron is greater in proportion.

#### *Coloration.*

The system of markings is similar to that met with in the *geometrica* group; the pattern, however, does not form regular stars, on account of the excentric positions of the areolars. These surfaces are reddish brown or rust-colour, black and pale horn-coloured bands radiating from them to the shield-edge; the rays are sometimes very strongly marked and regular, sometimes one colour predominating and sometimes the other, according to whether the black rays are broad or narrow, strongly marked or indistinct (*vide* Pl. I.). In the young the dark pigment is irregularly massed around each areolar. Each shield has its characteristic design, according to its contours; in well marked specimens that of the fifth vertebral resembles a rising sun, as depicted in decorative art; those on the marginals, the aster-pattern of old blue china.

On the plastron the system is the same, but the yellow or horn-colour greatly predominates, partly owing to the larger areolars and partly to the fact that the black rays do not always reach to the shield-edge.

The head and limbs are brownish or yellowish, sometimes indistinctly mottled.

Owing to the burrowing proclivities of these tortoises, the live specimens usually have their beautiful markings entirely obscured by dirt, which lodges in the deep concentric striations of the shields.

Mr. Loveridge notes that the specimens from Tabora are lighter in colour than those from Dodoma.

#### *Head.*

Head moderate; tympanum as large as or larger than eye: frontal usually broken up into four shields; praefrontal large, subcordiform, divided in one specimen; a pair of large supra-

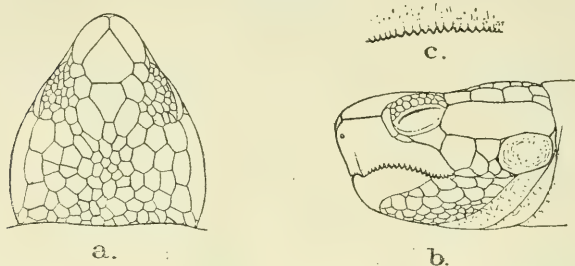
<i>Sex.</i>	<i>Length</i> in mm.	<i>Breadth</i> in mm. per cent.	<i>Depth</i> in mm. per cent.	<i>Abnormalities.</i>	<i>Collection.</i>
Yg.	42	45	33.4	Small intergular.	British Museum, N.H.
"	60	60	31.7	Nine ribs reaching marginal region on each side, <i>i.e.</i> supernumerary 10th pair.	"
"	71	64	29.6	Twelve marginals on each side.	"
H <sub>gr.</sub>	81	68	29.6	Supracaudal undivided.	"
"	85	77	...	Supracaudal undivided.	"
"	89	76	29.3	Supracaudal undivided.	Tring Museum.
"	103	87	23.3	Posterior marginals strongly serrated.	British Museum.
"	105	82	28.5	Supracaudal undivided.	Mus. Comp. Zool., Harvard
"	119	96	22.7	Supracaudal undivided.	British Museum.
"	130	100	21.5	Supracaudal undivided.	Loveridge Collection.
"	133	105	22.5	Supracaudal undivided.	"
"	135	120	...	Supracaudal undivided.	"
"	135	102	22.5	Supracaudal undivided.	American Museum, N.H.
"	137	108	22.5	Supracaudal undivided.	Mus. Comp. Zool., Harvard.
"	139	100	19	Supracaudal undivided.	Loveridge Collection.
"	140	110	20.8	Supracaudal undivided.	Zool. Society's Gardens.
"	140	110	...	Supracaudal undivided.	British Museum.
"	140	100	73	(Skeleton figured). Four vertebrae; fourth costals uniting by median suture behind third vertebral. Correlated abnor- malities in underlying bony plates.	" (type).
"	141	100	19.3	Supracaudal undivided.	"
"	142	107	20.6	Supracaudal undivided.	Loveridge Collection.
"	146	107	25.4*	Well-developed intergular (figured); twelve mar- ginals on left side.	Zool. Society's Gardens.
"	146	113	22.6	Supracaudal undivided.	Loveridge Collection.
"	149	115	22	Supracaudal undivided.	British Museum (type).
"	150	108	...	Intergular present, as large as a gular.	Tring Museum.
"	155	130	20	Supracaudal undivided.	Loveridge Collection.
"	160	130	...	Supracaudal undivided.	Smithsonian Institute.
"	160	130	83.8	Supracaudal undivided.	"
"	160	130	83.9	Supracaudal undivided.	"

\* This live specimen was greatly distended when measured.

nasals meeting each other by a mesial suture of variable length, usually between one-fourth and two-thirds length of præfrontal (*vide* text-fig. 2 a).

Horny coverings of sheaths of alveolar ridges of maxillæ and mandibles with regular, clearly-defined denticulations, 15 to 20 (usually about 20) on each outer, and 6 to 9 (usually about 7) on each inner maxilla; 12 to 15 on each outer and 5 to 9 or 10 on

Text-figure 2.



a. Upper surface of head. (Adult; nat. size.) b. Side view of head.  
c. Horny teeth enlarged.

each inner mandible. Beak tricuspid, with one or two of these denticulations between each cusp. Sometimes the points of these odontoids look precisely like the regular teeth of an Agamoid lizard; but in other individuals they are not so well developed. They may be more so in the upper than the under jaw, or on the outer or the inner ridges, but whenever distinct are extremely regular (*vide* text-fig. 2 b, c). In all cases they are more developed in the horn than in the underlying bone.

#### *Limbs.*

Lower part of fore-limbs covered with large claw- or scale-like shields, three very much enlarged on the anterior surface above wrist; normally five well-developed claws.

Tibial portion of hind-limb often longer than radial portion of fore-limb, covered with irregular juxtaposed horny shields the size of those on the humeral portion of the fore-limb; scales on sole enlarged and claw-like in adults; normally four strong claws. In an abnormal specimen these claws are so overgrown that the outer one measures 13 mm. A group of enlarged tubercles on hinder side of thigh in some individuals.

The limbs are not nearly so club-shaped as in most species of *Testudo*; both wrists and ankles are supple and defined by a well-marked crease in the skin; the foot projects considerably (*vide* Pl. I.). This is especially marked in the young.

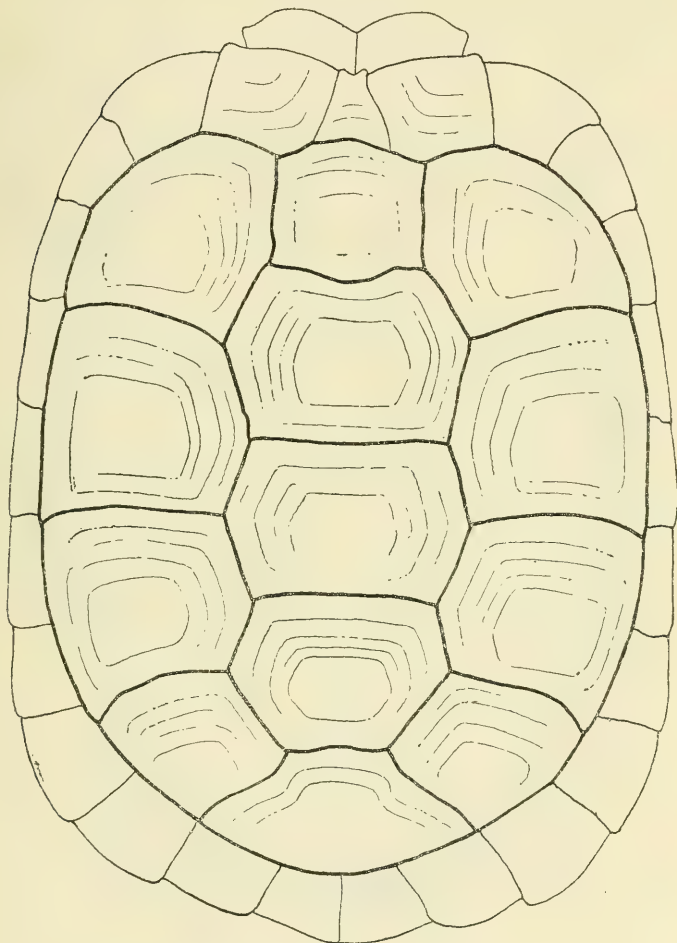
#### *Tail.*

Tail normal, much longer and stouter in the male than in the female.

*Epidermal shields.*

The epidermal shields are highly characteristic in form, but subject to great variation individually. In several specimens supernumerary shields and other abnormalities occur; for

Text-figure 3.

Epidermal shields of the carapace. (Adult;  $\frac{3}{4}$  nat. size.)

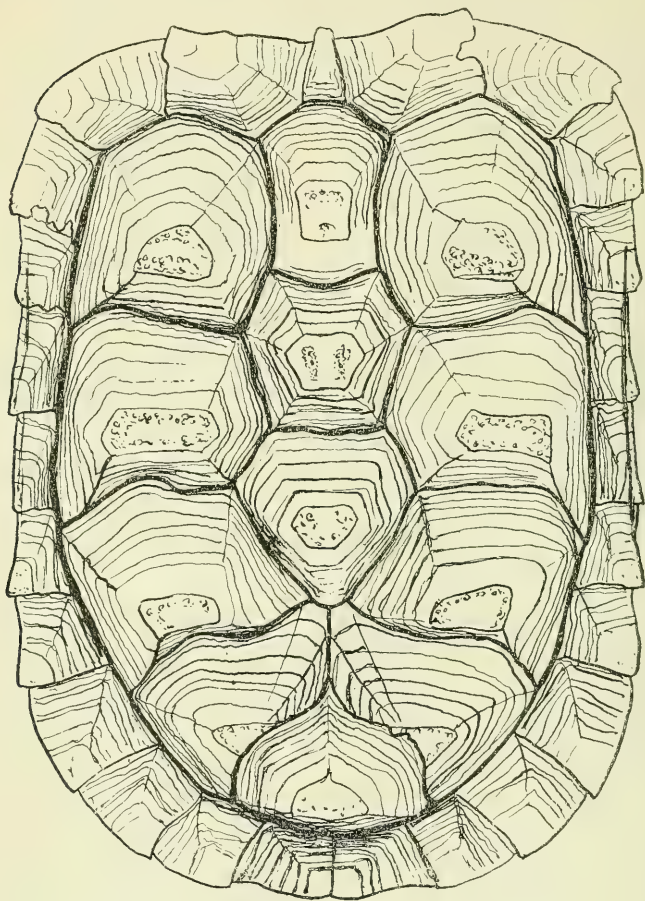
instance, one adult has twelve marginals on the left side, one has twelve on both sides, and in one the posterior marginals form a deeply serrated border; the male type has only four vertebrales, one female has the third vertebral divided longitudinally, and



two have extraordinary embossed vertebrals; three individuals possess an intergular. Mr. Loveridge mentions two specimens, which unfortunately escaped, in which small azygous shields occur, also several in which the supracaudal is single or semi-divided.

Each shield is also subject to considerable individual variation of size and shape.

Text-figure 4.



Sketch of carapace of male type-specimen, showing abnormalities in epidermal shields ( $\frac{3}{4}$  nat. size).

The shield surfaces in the young are excessively rugose or coarsely granulated, each one bordered narrowly by a raised band of smooth horn; with age these rugosities wear smooth, but the ensuing growth-rings, also of smooth horn, are extremely regular,

and the concentric striations between are deep and strongly marked. This applies to the plastron as well as the carapace.

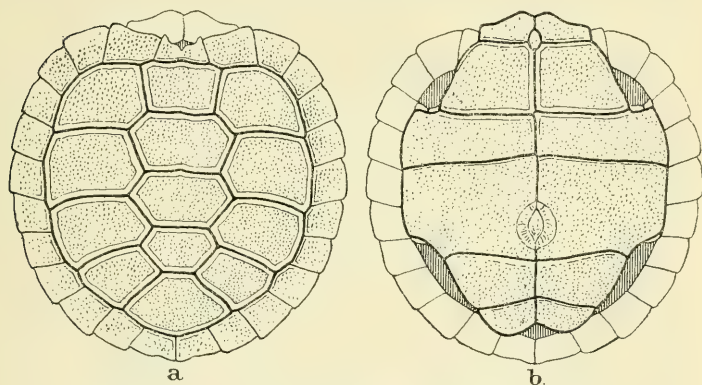
Nuchal shield very variable; much broader than long and cleft anteriorly in young specimens; about as long as broad to three times as long as broad, usually a little more than twice, and not, or but slightly, notched in adults.

First vertebral subtetragonal, usually slightly longer than broad, or as long as broad; the anterior border longer than the posterior, both convexly curved; lateral borders straight, slightly oblique. On the male type this shield is greatly elongated (*vide* text-fig. 4).

Second and third vertebrals hexagonal, broader than long, the suture between them usually a little shorter than the length of either shield, a little longer than the suture between first and second or third and fourth.

Fourth vertebral with very short posterior border, not more

Text-figure 5.



Young specimen, showing relatively broader shields (nat. size).

a. Carapace. b. Plastron.

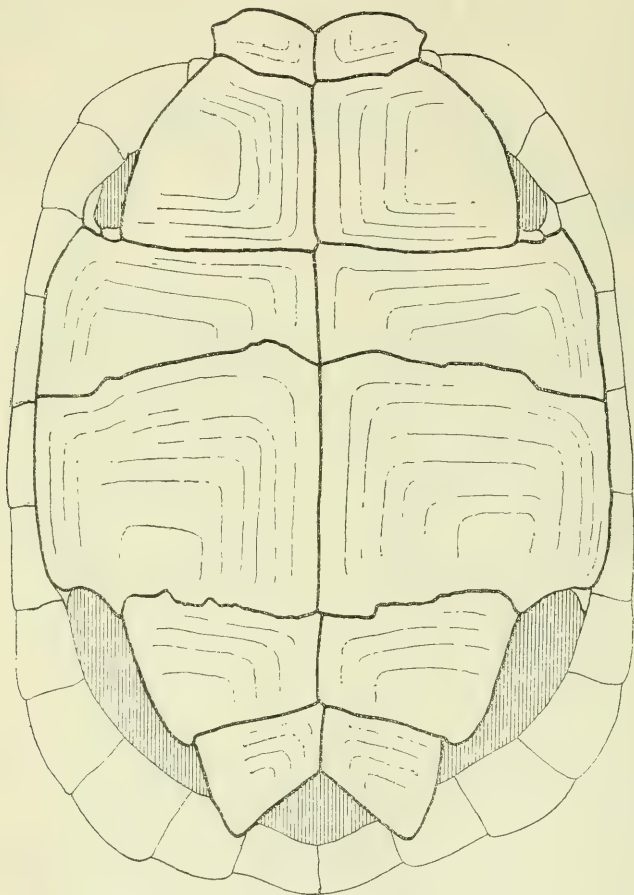
than half length of suture between third and fourth. In the male type this shield is subtriangular or cordiform, and widely separated from the last vertebral by the fourth costals.

Fifth vertebral obtusely pointed and flat anteriorly, in the same plane with the preceding vertebrals; posteriorly its border is curved, and bent downwards sometimes very abruptly; the lower edge in some cases curves in so as to form an angle with the more obliquely set supracaudals.

Costals highly characteristic in form. In the ordinary *Testudo* the sutures between these shields form straight lines more or less at right angles to the long axis of the carapace; in *T. loveridgii* they form curves, particularly pronounced in the case of those between the fourth pair and fifth vertebral. The areolars are also excentrically placed. In *T. ibera*, for instance, the border

around the areolar is about twice as broad in front as behind, and situated high up in the shield, the distance between it and the vertebrals being less than the distance between it and the costal posterior to it, and a quarter or less the distance between it and the marginals; in fact, the relative widths of the shield-borders

Text-figure 6.

Epidermal shields of the plastron. (Adult;  $\frac{3}{4}$  nat. size.)

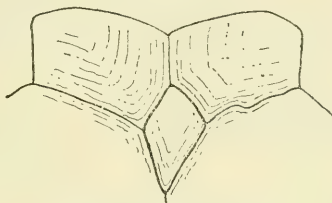
(top : back : bottom : front) are roughly expressed by the geometrical progression—2:4:8:16. In *T. loveridgii* this ratio is better expressed—4:2:4:5 or 4:1:4:6, the areolar being midway between vertebrals and marginals, but situated very far back in the shield. The areolar of the fourth costal is often

actually in contact with the anterior margin of the fifth vertebral. This condition is not marked in the young, but is accentuated by each growth-ring. The fourth pair, in the male type, as already remarked, are broadly in contact mesially, in front of the last vertebral; in no other instance does this occur although they are sometimes in close proximity. The abnormal form of these shields on the male type is shown in text-fig. 4.

The second costal is usually about equal in width to the third vertebral.

The marginals are also extremely characteristic and very greatly reduced in depth. The first pair are normal in outline but a little longer than deep; the second and third are about one and a half times as long as deep; fourth to eighth greatly reduced, once and a half to twice as long as deep, as against about two-thirds long as deep in *T. ibera*; ninth and (or) tenth deepest, a little deeper than long; tenth and eleventh similar but slightly smaller. In the young the marginals are more or less uniform, as deep as broad or a little deeper; the sutures dividing them are somewhat oblique, making them rhombic in shape (*vide* text-fig. 5 a).

Text-figure 7.



Intergular shield (nat. size).

The supracaudal is paired in all the specimens examined with the exception of a female living in the Zoological Society's Gardens, and three young specimens, in which it is single.

The epidermal shields of the plastron are not peculiar in any way (*vide* text-fig. 6).

Gulars moderate, truncate and rounded anteriorly, forming together a bow-shaped edge, projecting beyond the carapace and forming a support for the animal's chin; lateral edges shorter than the median suture; gulo-humeral sutures directed obliquely backwards and inwards, meeting each other at an angle of 60° to 140°.

An intergular is present in three out of twenty-three specimens. In the smallest specimen it is small but distinct (*vide* text-fig. 5 b); in one female it is somewhat smaller than a gular (*vide* text-fig. 7), and in a male it is well developed and as large as a gular. In all three it is protuberant and kite-shaped, the short sides in front.



Humeral about twice as broad at humero-pectoral suture as from apex to apex, or their median suture.

Pectorals narrow, median suture two-fifths to three-fifths length of median humeral suture.

Abdominals more or less square, median suture two to four times length of median pectoral suture.

Femorals very variable, median suture usually longer than median pectoral suture; postero-lateral corners projecting beyond lateral edges of anals.

Anals.—Ano-femoral sutures slightly oblique, directed forwards; lateral borders at right angles to them; median sutures short, each anal cut away posteriorly and ending in a pronounced point of variable shape, the resulting cleft between them forming an angle of  $90^{\circ}$  to  $120^{\circ}$ . The width and depth of this cleft is apparently not dependent on sex, as one would suppose from the great difference in the relative sizes of their tails.

The inferior surfaces of the marginals which cover the bridges are extremely narrow, from three to four times as long as deep.

#### SKELETON.

Besides the complete skeleton of one adult, and the radiographs of the types, a considerable amount of accessory material has been available. An excessively interesting individual, in which development had been arrested at a still earlier stage, decomposed in transit, thus enabling me to use most of the skeletal parts for study. In this specimen the bony plates were as thin as tissue-paper and extraordinarily flexible. Parts of other tortoises also disintegrated and formed interesting checks on the first skeleton.

Of the young, an X-ray plate shows that the limb-girdles are normal, as in the adult. The structure of the carapace has been studied in a series of six, ranging from 42 to 82 mm. in length; in these it was dissected off and the inside aspect cleaned. A complete preparation of both carapace and plastron was made from a specimen 60 mm. in length, and the plastron of the 42 mm. individual studied, without its removal, from the inside.

This material was amply sufficient to show the normal structure and development, besides some interesting variations of the skeleton of *T. loveridgii*, and to form highly interesting comparisons with other species.

The word "plate" is repeated after the name of each dermal bone, in order to distinguish them from the epidermal shields of the same names.

#### *The bony carapace of the adult.*

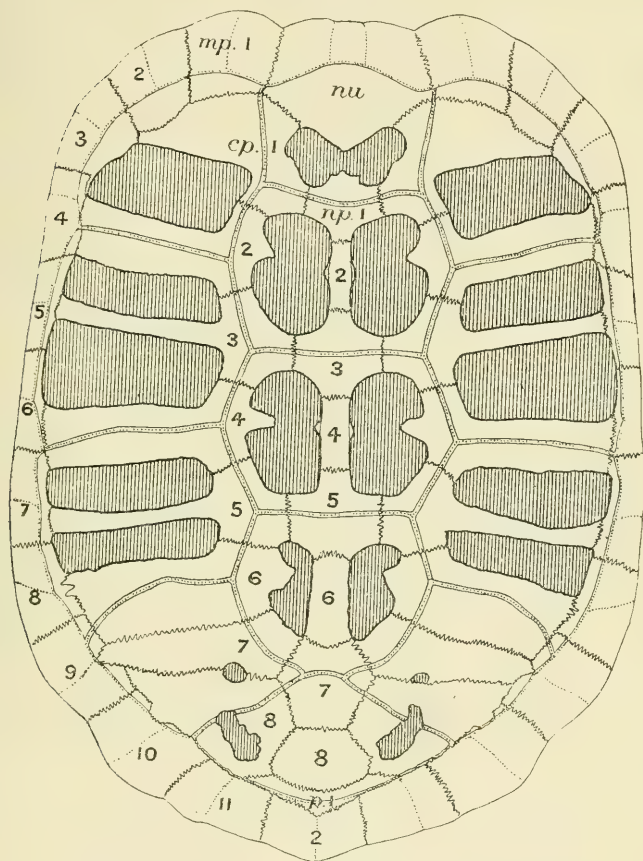
In general appearance the bony carapace is extraordinary. Such portions of the neural and costal plates as are present, are formed of translucent bone, and when damp are springy and flexible, making it possible to depress or elevate the carapace as if it were supported upon springs.



Where the epidermal shields form sutures with each other, the bone beneath is deeply grooved, sometimes forming perforations, but always markedly transparent (*vide* Pls. II. & III. and text-fig. 8).

Beneath the vertebral shields are four large fenestræ shaped like butterflies: the first is entire; second, third, and fourth

Text-figure 8.



Bony carapace of an adult, viewed from above ( $\frac{1}{5}$  nat. size).  
 Fenestræ |||||; deep grooves beneath shield-sutures ————; neural plates  
*np.*; costal plates, *cp.*; marginal plates, *mp.*; nuchal, *nu.*; pygals, *p.*

divided mesially each by a bony bridge formed of rudimentary neural plates; the first and fourth are small compared with the second and third (*vide* text-fig. 8).

Beneath the costal shields there are also large fenestræ similar in shape to the shields under which they are situated. That

under the first is entire; those beneath the second and third divided mesially by a narrow transverse bridge of bone formed by the third and fifth costal plates. There is no large fenestra beneath the fourth in the normal adult.

Nuchal plate moderate, posterior corner free, forming anterior edge of first median fenestra, which exposes the ninth vertebra.

First neural plate (text-fig. 8, *np. 1*) very much reduced in comparison with that of a normal *Testudo*; anterior edge pointed, bordering first fenestra by which it is separated from the nuchal plate; narrow lateral limbs, uniting by short sutures with first pair of costal plates (*cp. 1*); narrow posterior limb, entering into second median fenestra, where it forms part of the dividing bridge and unites by short suture with the second neural.

Second neural plate (*np. 2*) vestigial, barely wider than the vertebræ beneath, with straight lateral edges, uniting by short sutures with preceding and succeeding neurals, and forming the main part of the fenestral bridge.

Third neural plate (*np. 3*) octagonal, very much reduced, oblique edges free, curved invertedly, bordering the inner corners of the second and third fenestræ, which this plate divides one from the other by uniting with the second costal plates (*cp. 2*) by narrow sutures, thus forming a narrow bridge between them; also forming similar connections with second and fourth neurals.

Fourth neural plate (*np. 4*) similar to second but somewhat broader in proportion, forming the longitudinal dividing bridge across the third median fenestra.

Fifth neural plate (*np. 5*) precisely similar to the third.

Sixth neural plate (*np. 6*) similar to second and fourth but broader still, dividing fourth median fenestra, which is, however, much smaller than the two preceding.

Seventh neural plate (*np. 7*) normal, hexagonal, without free edges, uniting by six sutures with the sixth and eighth neural, and seventh and eighth costal plates respectively; those formed with the eighth costals slightly longer than the others.

Eighth neural plate (*np. 8*) normal, sub-tetragonal, without free edges, uniting by oblique sutures with the eighth costal, and by transverse ones with the seventh neural and first pygal plates, the latter suture the longer and curved.

First pygal plate broadly cordiform or septagonal, set almost at right angles to the horizontal plane of the neurals, curving in where the marginal epidermal shields meet the fifth vertebral, and curving out more obliquely to form a point beneath the supra-caudal shields. It forms sutures with the eighth neural and costal, eleventh marginal (*mp. 11*), and second pygal (*p. 2*) plates, that with the eighth neural about twice as long as any of the others and curved invertedly.

Second pygal normal, equal in size to the eleventh marginal plate.

First costal plates (*cp. 1*) shaped like wings, uniting by short sutures with the lateral edges of first neural (which forms a

bridge between them) and second costal plates, thus separating the first lateral fenestra from the first and second median fenestræ on each side; the broadly curved anterior edges form an uninterrupted suture with part of nuchal, whole of first and second, and inner corner of third marginal plates in most cases, but sometimes the distal portion is undeveloped, and therefore less wing-like, or cleft, or perforated beneath the shield-sutures (*vide* text-fig. 9).

Text-figure 9.



Left first costal plate from beneath, showing perforation beneath vertebro-costal shield-suture; distal end incompletely developed, and cleft. (Nat. size.)

Fenestræ between first and second costal plates are from front to back as long as one marginal, from side to side two or three times this length.

Second costal plates (*cp.* 2) slender, feebly developed, widely separated from the neural; anterior and posterior heads forming narrow sutures with first and third costal plates beneath costo-vertebral shield-sutures, main arms supporting transverse costal shield-suture, and uniting distally with the fourth marginal plate. Length of each (measured from end to end) three times breadth (measured from front to back); median head forming a short-pointed process directed inwards, but widely separated from the vestigial second neural plate. The X-ray plates of the types show that these processes are sometimes connected with the vestigial rib-heads by the ligament-like periosteal tissue of the absorbed rib.

Third costal plates (*cp.* 3) extremely slender, rib-like, and feebly developed. Main arms half or less than half breadth of those of second, from which they are separated by a fenestra about half as broad as those preceding. Each has three heads, each one of which is twice as broad as the main arm, the median uniting by suture with the third neural plate, thus forming a bridge between second and third median fenestræ on each side; anterior and posterior heads directed obliquely outwards, similarly united with the corresponding heads of second and third costal plates, which are directed obliquely inwards beneath the costo-vertebral shield-sutures.

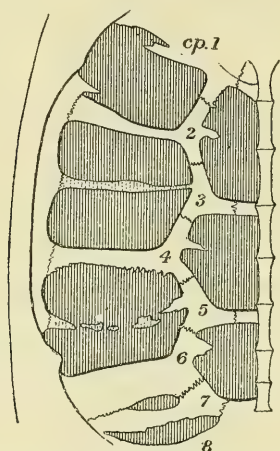
In the specimen in which development has been arrested at a

very early stage, only the merest traces of bone-deposit are present in place of the rib-like arms of these plates (*vide* text-fig. 10).

Fourth costal plates (*cp.* 4) in form precisely like second, twice or more than twice width of third, sometimes with very ragged edges; widely separated from neural by third median fenestræ, forming a suture with sixth marginal plates, sometimes with corner of seventh also. Fenestra between third and fourth similar in size and shape to that between first and second, about twice width of that between second and third.

Fifth costal plates (*cp.* 5) precisely like third in every way, connecting by suture with seventh marginal plates. Fenestra

Text-figure 10.



Carapace of adult arrested at an earlier stage in development.  
(Left side, from within;  $\frac{1}{2}$  nat. size.)

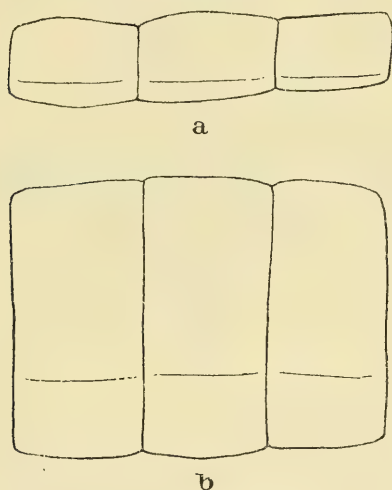
between fourth and fifth similar to that between second and third, about half width of that between third and fourth. In the poorly developed specimen already referred to (text-fig. 10) the rib-like limb is represented by a few bone-granules in isolated patches.

Sixth costal plates (*cp.* 6) similar to second and fourth, but rather more developed. Anteriorly narrowly in contact with fifth beneath the vertebro-costal shield-sutures, otherwise separated by fenestræ slightly narrower than any of the preceding. Central head in closer proximity to the neurals than those of second and fourth; the dividing fenestra about half as large as in the former instances. Posterior edge quite straight, forming

a suture with seventh costal plate throughout its length from fenestra to ninth marginal, excepting in the abnormal specimen, in which it is partially separated from the seventh by an elongated fenestra.

Seventh costal plates (*cp. 7*) straight, with angular head and pointed distal end which is projected some distance into middle of ninth marginal. Anterior facet of head free, bordering fourth vertebral fenestra, posterior forming suture with seventh neural plate; main anterior border forming suture with sixth costal from end to end, posterior border forming a similar suture with eighth. On the upper third of the suture between the seventh and eighth costal plates there is a small oval fenestra,

Text-figure 11.

Diagram of marginals 5, 6, and 7. a. *T. loveridgii*. b. *T. ibera*.

smaller on one side than on the other in the individual figured, but of variable size in others. It is always very ragged in outline.

Eighth costal plates (*cp. 8*) pentagonal, broad, with the exception of the very small fenestra described above, completely in contact with the surrounding plates—*i. e.*, seventh costal, seventh and eighth neural, first pygal, ninth, tenth, and eleventh marginal plates. A small triangular process is projected into the anterior portion of tenth marginal. A small kidney-shaped fenestra with jagged edges pierced above the ilio-sacral region, anteriorly reaches just beyond the groove made by the fourth costal and fifth



vertebral shields and proceeding backwards almost to the eighth neural.

Presumably this fenestra and the small oval one between the seventh and eighth costals are all that remain of the large kidney-shaped one, similar to those between the preceding costal and neurals, which is present in youth.

The marginal bones are somewhat wider than the corresponding shields; first, second, and third markedly so; sixth to tenth deeply notched in the middle for the reception of spurs from the corresponding costal plates. Fifth, sixth, and seventh enter into the composition of the plastron beneath, and will be dealt with as part of the plastron.

When one considers the great depth of the lateral marginals in ordinary tortoises in comparison with their abnormal shallowness in *T. loveridgii*, the shallow carapace of the latter is to some extent explained. In text-fig. 11 the fifth, six, and seventh marginal plates, drawn diagrammatically, of *T. loveridgii* and *T. ibera* are compared.

*The bony plastron of the adult.*

The bony plastron is also composed of bone thin to translucency. In the centre there is an enormous diamond-shaped fenestra reaching from ento- to xiphiplastron, and side to side from marginals to marginals. It is very ragged in outline, variable in size, and lies beneath the pectoral and abdominal shields, so that the greater part of the abdomen is unprotected by bone (*vide* text-fig. 12).

Epiplastrons (*ep.*) shapely, oblique, moderate in size; posterior borders serpentine.

Entoplastron (*ent.*) in the shape of a diamond, the anterior and posterior corners of which have been truncated; posterior margin free, corresponding with the humero-pectoral shield-suture above, entering into the central fenestra, into which a sharp bony spur projects, representing the tip of the sternum, which is fused to the inner surface of this plate in the normal way.

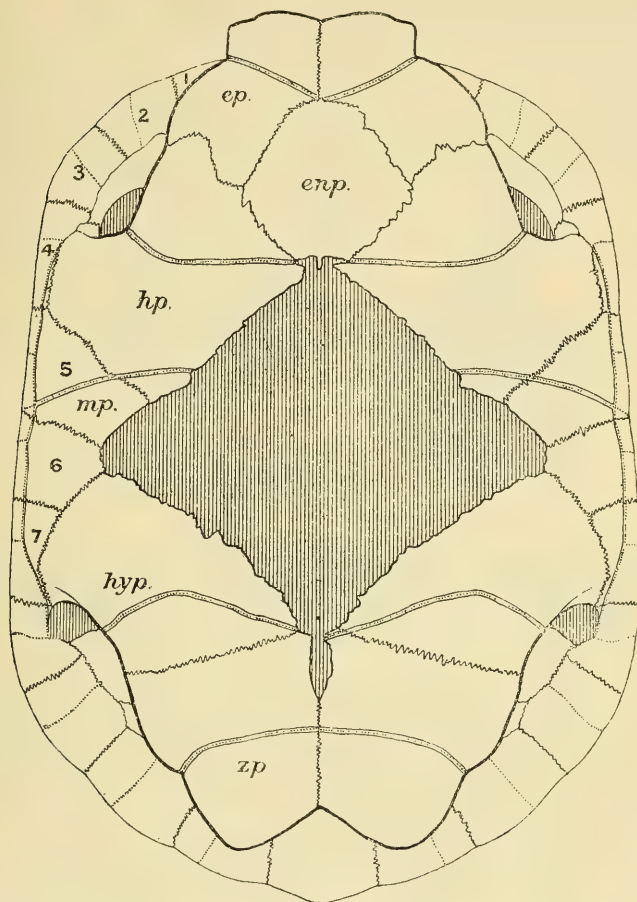
Hypoplastrons (*hp.*) very small, rectangular, obliquely set; separated from each other by the anterior angle of central fenestra; widely separated from the hypoplastrons by marginal plates.

Marginal plates (*mp.*) 5, 6, and 7 enter into the composition of the plastron on each side of the fenestra, spreading obliquely inwards to a most unusual degree, number 5 running beneath the pectoral shields to the abdominal, and terminating with a free oblique edge in the central fenestra; number 6 borders the lateral corner of the central fenestra on each side.


Hypoplastrons (*hyp.*) completely separated from each other by the posterior angle of the central fenestra; produced to form part of the posterior plastral lobe.

Xiphiplastrons (*zp.*) form slightly oblique sutures with the hypoplastrons; their anterior median corners enter into the

Text-figure 12.



Bony plastron of an adult, viewed from without ( $\frac{4}{5}$  nat size).

Fenestra ||.||; deep grooves beneath epidermal shield-suture \*; epiplastrons, *ep.*; entoplastron, *enp.*; hyoplastrons, *hp.*; hypoplastrons, *hyp.*; xiphiplastrons, *zp.*; marginal plates, *mp.*

posterior corner of the central fenestra, which separates them from each other anteriorly; a broad open cleft posteriorly; lateral edges bi-lobate.

\* The groove beneath the median longitudinal shield-sutures is equally deep, but is not marked, as it would obscure the bony ones beneath.

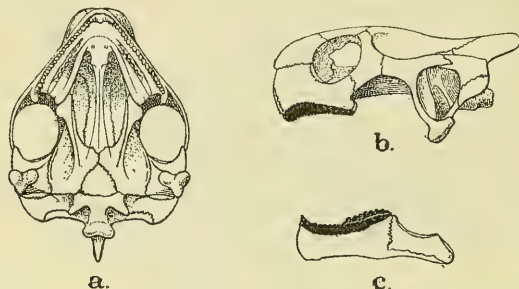
*Skull.*

Differing from the common *T. ibera* in the following particulars:—

The præfrontals are larger than the frontals, and widely separated from the post-frontal bridge; temporal and post-orbital arches stouter in proportion, especially the latter; *annulus tympanicus* larger, stapes as slender as a hair.

Maxillary with three alveolar ridges, the inner one of which is comparatively weak, the outer one, or maxillary edge, denticulated with what appear to be minute pointed teeth of the acrodont type, but which have not the composition of true teeth; the number is about 20 on each outer, and about 7 on each inner, maxillary

Text-figure 13.



Skull of adult (nat. size). *a.* Palatal view (horny sheaths not blackened). *b.* Side view (horny sheaths blackened). Horny sheath of maxillary partially dissected away to show denticulations in the bone itself. *c.* Mandible (horny sheaths blackened).

ridge. One or two similar denticles between the cusps of the præmaxillary. These denticles are so fragile that if the adherent horny sheath is removed in the usual way, they are completely destroyed, but they can be clearly seen without a lens if the horn is partially removed. In text-fig. 13 this has been done, and the remaining horn blackened in the profile view, in order to distinguish it from the maxilla.

All the cranial foramina seem to be proportionately small.

The mandible has both its alveolar ridges denticulated in the same manner as the maxilla. In the figure the horny sheaths, in this case entire, are blackened.

*Vertebral column.*

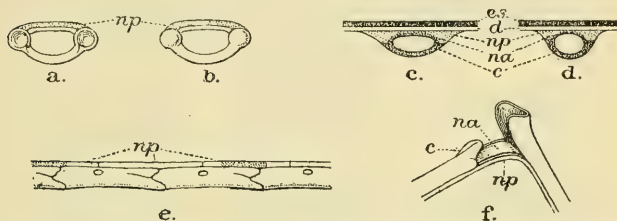
First eight (cervical) vertebræ as in *T. ibera*.

The dorsal vertebræ (ninth to eighteenth in the complete series) differ profoundly from the ordinary pattern; they are entirely without spinous processes and the centra are greatly depressed instead of compressed, and hollowed to a thin shell for the reception of the spinal cord, the vertebræ being thus a simple depressed tube, adherent to the bony neural plates of the carapace. In all other species the vertebral column is separated

from the carapace by wide arches, the contact with it being formed by long thin neural processes; in no case is the main column, even narrowly, in contact (excepting *T. tornieri*).

It is in some cases impossible to detect what remains of the neural arch in a section, for it has degenerated to such an extent that in some individuals it appears to be wanting altogether. Possibly it is absorbed to a variable extent in the same manner as the ribs. In the vertebral sections figured (*vide* text-fig. 14), it seems to be represented by an extremely thin layer beneath the neural plate, forming a meagre roof to the neural canal. The specimen to which it belongs, however, is the most degenerate of any that have been examined. More normal individuals, however, cannot be spared for the necessary dissection. Figs. c and d show diagrams of sections through the middle and towards the anterior end of the eleventh vertebra;

Text-figure 14.



Diagrams of mid-dorsal vertebrae. a. Anterior end. b. Posterior end. c. Section towards one end. d. Section through middle. e. Side view of vertebrae with lateral expansions of neural plates cut off. f. Two vertebrae bent apart, to show thinness and flexibility of the combined neural plate and neural arch. Epidermal shield, *es*; dermis, *d*; neural plate, *np*; neural arch, *na*; centrum, *c*.

figs. a and b, the vertebra viewed from each end; fig. e, the twelfth and thirteenth with part of eleventh, side view, with the lateral portion of the third neural plate cut through; fig. f, the twelfth and thirteenth, bent apart to show the thin flexible covering of the neural canal. The relative positions of the articulation of the vertebrae and the neural plate sutures vary, usually alternating with each other. The points of juncture between the 5th and 6th neural plates and 14th and 15th vertebrae, however, coincide, one above the other.

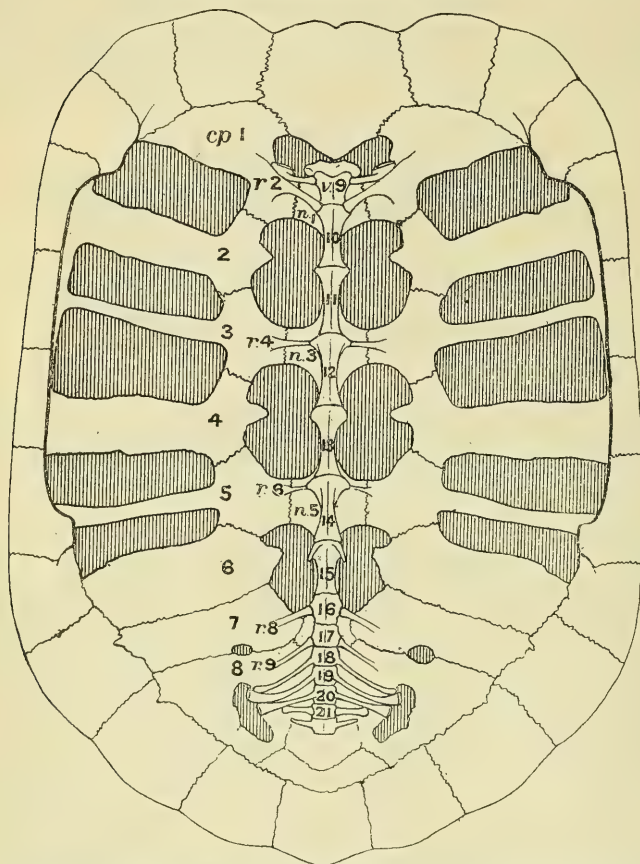
The ninth vertebra is, of course, highly specialised for the articulation of the neck. The facets for the articulation of the first (non-functional) ribs are situated at the extreme anterior end. Vertebrae ten (2nd dorsal) to thirteen are progressively more elongate, and have the tubercles for the articulation of the rib-heads at the extreme anterior end on each side as in the ninth; in some of the young, articulation takes place at the juncture of each consecutive pair of vertebrae. Fourteenth to seventeenth become progressively shorter, and the facets for the corresponding rib move further backwards in a lateral ridge as the ribs become directed obliquely in this direction. Eighteenth



nineteenth, twentieth, and twenty-first vertebræ progressively shorter, their diapophyses elongate, slender, distally in contact and supporting the iliac crests, those of the nineteenth the longest. Diapophyses of anterior caudal vertebræ also elongate. Caudals normal, twenty-four in number, stouter in the male than in the female, according to the radiographs.

### *Ribs.*

The ribs may be considered as absent in the adult, the part  
Text-figure 15.



Bony carapace of an adult, from within ( $\frac{2}{3}$  nat. size), showing vertebræ, and vestigial ribs. (Ribs not entirely absorbed in this specimen.)\*

normally adherent to the carapace having become completely absorbed. The free or capitular portion is sometimes present as

\* Sutures between costal plates 2, 3 and marginal plates 4, 5, accidentally omitted.



a vestigial thorn-like structure, but is more often absent altogether, or represented by a thin ligamentous simulacrum (*vide* Pls. II. & III.).

The first pair, which in all tortoises are rudimentary, are normal. The second (first functional) have the free capitular portion sometimes present, although reduced, adherent terminally to the first costal plate, and in contact with the first pair in the usual manner (*vide* text-fig. 15). Third pair absent or vestigial.

Fourth pair, when present, similar to the second, but usually as slender as a hair; in contact with third pair of costal plates. Fifth pair absent or vestigial. Sixth pair like the fourth, but still more vestigial and directed slightly backwards. Seventh pair absent or in some specimens present, and bridging the fenestræ and meeting the corresponding process of the sixth costal plates, directed slightly backwards. Eighth pair rather depressed, directed still more backwards, in contact with the seventh pair of costal plates just in front of the seventh neural plate. Ninth pair slender, directed strongly backwards and flattening out beneath the head of the eighth costal plates.

In the young specimen (60 mm. long) described in the next chapter, a tenth pair of ribs are present.

#### *Pectoral girdle.*

The bones of the pectoral girdle and fore-limbs, as compared with those of *T. ibera*, are slender, and the coracoids are not so strongly dilated; in other respects they are similar (*vide* Pls. II. & III.).

#### *Pelvic girdle.*

The bones of the pelvic girdle and hind-limbs, also compared with those of *T. ibera*, are somewhat more slender and those of the pelvis less dilated (*vide* Pls. II. & III.). The ilia are not fixed above as in the ordinary tortoises, as they terminate just beneath the last median fenestræ in the carapace, whilst in tortoises with a solid carapace they articulate with a bony prominence beneath the eighth costal plate.

### DEVELOPMENT.

Until April of this year, only adult or extremely young specimens were available, and it was, therefore, only possible to guess at the intermediate skeletal forms. Mr. Loveridge has, however, now sent over a series of young and half-grown, which illustrate the processes which are taking place and corroborate my earlier speculations.

#### *Ribs.*

In the young the ribs are perfectly normal (*vide* text-figs. 17, 18) but step by step they disappear. The portion adherent to the carapace becomes flattened, and disappears in a manner similar to that met with in other members of the genus. The first portion to become completely absorbed is that which underlies

the oblique connecting bridges between the costal plates, which in turn underlie the vertebro-costal epidermal shield-sutures: that is to say, the point where the rib becomes adherent.

The capitular free portion of the rib absorbs in a peculiar way. At 71 mm. these free ribs still appear to be present when the carapace of a spirit specimen is raised; when explored, however, they prove to be chiefly composed of soft pliant material, like ligament. At 81 mm. there is still a splinter-like rib within this soft material, but this becomes more and more wasted by absorption, until it is lost absolutely in the adult, or represented by a tiny thorn-like splinter one or two mm. in length—the extreme capitulum of the original rib. Mr. Burne has very kindly investigated the structure of this soft portion, excised from a young specimen. Longitudinal sections show that with

Text-figure 16.



Microscopic section through capitulum of absorbing rib ( $\times 100$ ), in which almost nothing but periosteum is left. (After a sketch by Mr. Burne.) Periosteal fibres, *p*; cartilage, *c*; areas of calcification, *b*.

the exception of two small areas of calcification in the capitulum itself, no bone is left (*vide* text-fig. 16). These areas are situated in a part of the original cartilage; the rest of the section shows nothing but parallel bundles of what appears to be connective tissue. Near the edge of the sections there are, however, a row of multi-nucleated cells which Mr. Burne considers to be osteoclasts. He says: "I presume what happens is that the bone after being formed in the rib is absorbed by these osteoclasts, and the periosteum—possibly thickened—is left, forming a simulacrum of the rib." There is no doubt in my mind that this is the right interpretation; also that this process of absorption, carried only to an early stage, is responsible for the excessive slenderness of this portion of the ribs in other species.

#### *The carapace.*

In a specimen 42 mm. in length, probably newly hatched or only a few months old, the plates are commencing their development, and are at a particularly interesting stage (*vide* text-fig. 17).

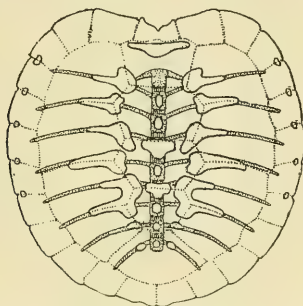
The nuchal is more or less fully formed within the marginal ring, but does not extend beyond. The neurals, excepting the third and fifth, consist of minute oval areas of yellowish bone-granules towards the anterior of each underlying vertebra. The third and fifth are laterally dilated to some extent, the fifth being almost in contact with the head of the fifth costal plate. These two neurals underlie the two middle vertebral shield-sutures. The thin layer of coarse bone-granules which composes each

one of them is distinguishable without a lens. In pulling up the carapace, quite half of these plates separated easily from the vertebræ and adhered to the carapace, or rather to the dermis, which shows that they are not completely fused with the vertebræ at this stage.

The costals are slightly more developed, and are disposed as follows:—The vertebral and costal epidermal shields meet each other in a zigzag suture which has seven angles. At each of these, three shields meet corner to corner. It is beneath these points that the centres of the incipient costal plates are located. They are therefore alternately nearer to, and further from, the vertebræ. Those nearer to them tend to develop proximally, and are more or less rhomboidal in shape, and those further away develop distally down the rib, and are more triangular, the apex pointing towards the marginal region.

The first, second, and third are not quite in contact with each other, the third, fourth, and fifth are nearly in corner to corner

Text-figure 17.



Carapace of newly-hatched young, from without (nat. size).  
Epidermal shield-sutures .....; vertebræ and ribs :::::

contact, the fifth and sixth are joined by oblique suture as in the adult, forming an oblique bony bridge beneath the shield-suture. The seventh and eighth are but commencing their formation.

The pygals are absent altogether.

The marginal plates are not recognizable as such at this stage, but minute groups of bone-granules are detectable beneath the shield-sutures between marginals three to eight. Posteriorly they are not visible, although their primary particles may be present in the dermis.

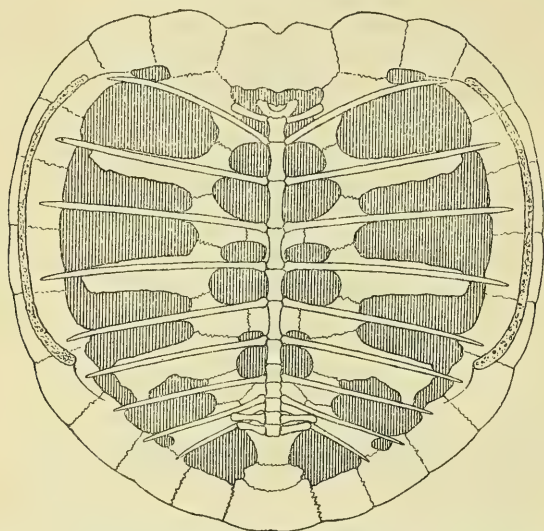
At about 60 mm. the eight pairs of ribs (2nd to 9th) are still distinct and of normal length, but are modified, the proximal 5 mm. having become very slender, and the remainder flattened and adherent to the dermal costal plates where these are present. In the particular specimen figured a ninth pair of ribs are fully developed, and reach the marginals on both sides.

At this stage (*vide* text-fig. 18) the development of the

dermal bones of the carapace is well advanced, showing most clearly how the carapace of the adult is formed. The anterior and median portion is developed almost as much as in the adult, but posteriorly large fenestræ occur beneath the fourth costal and fifth vertebral shields, which (fenestræ) are almost entirely roofed in with bone in the adults.

The nuchal and marginal plates are fully formed. The neurals are of the adult pattern, but they are narrow, thin, and feebly developed anteriorly, becoming progressively broader posteriorly, the seventh and eighth are the broadest, followed by a much narrower first pygal. The first pygal is not well developed, and is separated from the last costal plate on each side by a very wide,

Text-figure 18.



Carapace of young specimen 60 mm. in length, from within ( $\frac{7}{8}$  nat. size).

subtriangular fenestra, which is represented in the adult by a small one of ragged outline in the last costal plate itself.

From the study of this one stage it is easy to reconstruct the development of the bony carapace of the adult, and, by logical conclusion, to suggest a manner in which a solid carapace can be formed.

Costal plates one to six are similar in form and arrangement to those of the adult, excepting that they do not reach the marginal rib by about 3 mm. In the case of the first, the shortness of the plate causes a small fenestra to be discovered between the underlying rib and the anterior marginal plates.

At this stage one sees the relative positions of true ribs and



costal plates, which are not clear in the ribless adults. The main limbs of the second, fourth, sixth, and eighth costal plates are very broad, narrowly bordering the underlying rib anteriorly but projecting widely beyond its posterior edge. The alternating third, fifth, and seventh are but feebly developed, and are very little broader than the underlying rib, which they cover, and border narrowly and equally. This alternating arrangement of the breadth development, which takes place posterior to the companion rib, accounts for the relative widths of the lateral fenestræ in the adult, in which the slender costal plates are preceded by a narrow fenestra, and succeeded by one at least twice as broad, the general effect being a single fenestra the shape of the epidermal shield, bridged by a slender rib-like costal. The same principle applies to the formation of the plates beneath the vertebral shields. In this case the first, third, fifth, and seventh neurals are well developed (progressively as already noted), and form lateral sutures with the corresponding well-developed heads of the corresponding costal plates. The broad bridge of dermal bone thus formed is over and posterior to the free underlying rib-head. This makes the segment of the median fenestra immediately following, half the width of the remaining segment on each side of the vertebræ, a similar arrangement to that met with in the case of the lateral fenestræ. The alternating second, fourth, and sixth neural plates are feebly developed, barely wider than the underlying adherent vertebræ, and are widely separated from their corresponding costals, which, though they are broadly developed distally, are not continued proximally. The large kidney-shaped fenestra in the dermal bone is, however, bridged by the true rib beneath; a slight deposit of dermal bone on the distal end of this rib-bridge forms the feeble, pointed apical head of the costal plate which projects into the fenestræ at a later stage when the rib itself has absorbed.

Thus the broad neuro-costal bridges are continuous with the slender main-limbed costals, and the undeveloped neurals are connected by the free portion of the rib with broad costal main limbs. The bony bridges formed by the oblique heads of the costal plates, and which separate the median from the lateral fenestræ (beneath the vertebro-costal epidermal shield-sutures), are about as wide as their neighbouring broad costal or neural plates. In the same way narrow anterior sections of the median fenestræ are opposite the wide and posterior sections of the lateral fenestræ, and *vice versa*.

In the young of this size there is one great difference in the stage of dermal bone development, namely that of the seventh and eighth costal plates. In the adult, the seventh, although narrow, normally forms an uninterrupted suture with the sixth and eighth from the last median fenestra to the marginal region. At the present stage, the seventh is similar to the slender third and fifth costals, and the eighth is similar to the broad second, fourth, and sixth costals, the seventh being separated from the eighth by a wide



fenestra, represented in the adult by a small fontanelle, and from the sixth by a narrow one, absent in the adult; the latter fenestra, however, is divided into two by the contact of the posterior corner of the end of the dilated sixth with the seventh costal, about 3 mm. from the marginal plates. This is caused by the relative positions of the implicated ribs, which become closer together posteriorly as the vertebræ become progressively shorter. For this reason, the eighth costal plate in this specimen completely roofs over the ninth and tenth (abnormal) ribs, the intervening space between them being no broader than the entire second costal plate (compare text-figs. 18 and 15).

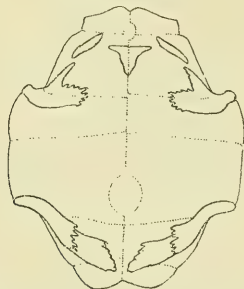
Therefore, in the first instance (42 mm.) it is the central portion of the carapace which is the most developed; later (60 mm.) the plates are more or less equally developed all over, with the exception of the neurals, which are progressively enlarged posteriorly. Continuing up the series (71, 81, and 89 mm.), the first, second, fourth, sixth, and eighth costal plates expand in length until they form sutures with the marginals; the third and fifth become the slender rib-like plates of the adult form; and the posterior portion of the carapace from the seventh costal to the pygal plates becomes roofed in with bone by the expansion of the seventh and eighth costal plates.

The anterior part of the carapace in the adult, therefore, is arrested at an earlier stage in its development than the posterior.

#### *The plastron.*

At 42 mm. the plastron is in the initial stage of development (*vide* text-fig. 19); all nine bones are present, but very small, thin, and for the most part widely separated from each other. The epiplastrons are merely small strips of bony deposit beneath

Text-figure 19.



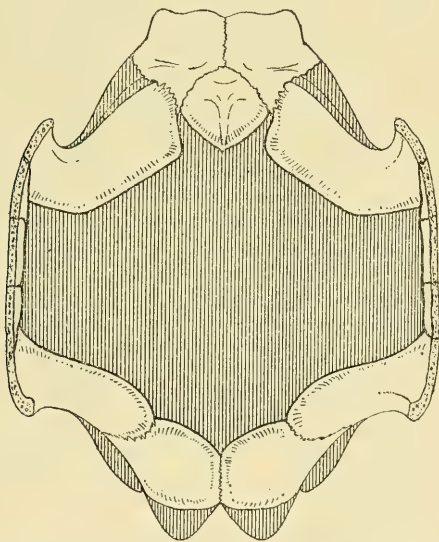
Plastron of newly-hatched young, from without (nat. size).

the anterior portion of the pectorals. The entoplastron is better developed, and subtriangular in shape. The hyoplastrons are ragged in outline, and not in contact with epiplastrons or

entoplastron. Hypo- and xiphiplastrons narrow and in sutural contact, forming a narrow, bony band running obliquely across the hind lobe. The xiphiplastrons, however, do not meet each other.

In the 60 mm. specimen (*vide* text-fig. 20) the median fenestra is much broader in proportion than in the adult, reaching almost from edge to edge of the plastron. Marginal plates five, six, and seven, which in the adult are produced inwards for a considerable distance, only overlap the line of their corresponding epidermal shields to a small extent, and are about equal, not graduated in depth as in the adult (*vide* text-figs. 12 & 20). The epiplastrons are more or less pentagonal and not well developed posteriorly at their outer corners, but are in contact with the

Text-figure 20.



Plastron of young specimen, 60 mm. in length, from within (nat. size).

hyoplastrons and the entoplastron. Hyoplastrons narrow and not in contact with the entoplastron, or with the fifth marginal plates, with which in adults they form long oblique sutures. Hypoplastrons slender, widely separated from each other, and only narrowly in contact with the sixth marginal plate; they form short sutures with the equally slender xiphiplastrons.

Further development takes place principally on the inner borders of the plastral plates until the central fenestra has assumed the regular diamond-shaped form of the adult in this species (compare text-figs. 19, 20, and 12).

## DISCUSSION.

*The morphogeny of the carapace and plastron.*

The primitive plastron, therefore, and the delicate network of dermal bone which forms the carapace of the adult *Testudo loveridgii*, are brought about by arrested development. The fenestræ have not been formed in the completed structures by absorption, and do not increase in this manner with age as supposed. The relative thickness or breadth of the plates depends on individual variation, specimens of abnormal fragility having had their development in this respect cut short at an earlier stage than the average individual. This principle also applies to such species as *Testudo polyphemus*, in which the carapace is said to become thin and form fenestræ with age. A specimen in the British Museum Collection of 210 mm. (76.1.36.6) and a half-grown specimen of 135 mm. (73.8.13.25) have both carapaces and plastrons fenestrated in a manner similar to those of *T. loveridgii*, whilst one of 225 mm. has them thin but entire.

The ribs of the latter on the other hand, and seemingly the neural arch of the vertebræ, do absorb with growth; the ribs completely in most cases. Thus the bony plates are developing, whilst the ribs are degenerating by osteoclastic absorption—a process which is, of course, physiological, and in fact, as far as the ribs are concerned, carries to a logical conclusion a tendency which is well marked throughout the genus.

The question which now arises is: what has led to the extraordinary degree of depression of the carapace? Some individuals are positively concave above, and all have a markedly deformed and rickety appearance.

Flattening is evidently not brought about, at any rate to this extent, by a fenestrated or thin condition of the carapace, for the giant tortoises which pass through these stages in the course of development and have very thin carapaces, are remarkably convex in form. The only visible result here is the crumpled appearance of the shell of *T. abingdonii*. *T. polyphemus*, on the other hand, is distinctly flattened.

It can be argued on the one hand that the flattened carapace is brought about by the habit of living beneath stones and squeezing into rock-crevices. This habit, induced by environment, would be bound to have a modifying effect; for, during youth, the development of a domed and solid carapace would be interfered with by the constant application of pressure, and in a sufficient number of generations the ability to form a normal carapace might be lost altogether. The fact that the Burrowing Tortoise, *T. polyphemus*, has a thin or fenestrated and somewhat flattened carapace supports this view. Could this be proved experimentally, it would furnish a convincing argument in favour of the heritance of acquired characters.

On the other hand, it can be equally well maintained that an inherited tendency to the arrest in development is

orthogenetic, brought about either gradually or as a mutation, and that the furtive habit of hiding beneath stones was the natural result, since the tortoise no longer possessed adequate protection from enemies.

Possibly both principles come into play, the reduced armour and loss of ribs being orthogenetic, and the depression and relative condition of the vertebræ being subsequently induced by the rock-dwelling habit.

Again, the metabolism of bone formation may be to some extent influenced by climatic conditions, lack of lime in the soil or water etc., or by their food. In this connection it is interesting to note that Mr. Loveridge has recently found two specimens of *Cinixys belliana* in the *T. loveridgii* locality which have remarkably depressed carapaces (31% of total length as against over 40%); and, further, Tornier describes one from Bussisi, the *T. tornieri* locality, which has its bony plates excessively thin, and actually fenestrated. Possibly this individual, if let alone, might have founded a race of soft-shelled tortoises in this genus also.

The actual process of development of the bony plates of both carapace and plastron in *T. loveridgii* is really quite normal; in spite of the astounding appearance which they present in the adult, they are similar in general form to those of the young of other species. In some, of course, one set of elements may develop more quickly in proportion, altering the balance of the fenestræ or their outlines, but the same process is gone through by them all.

On dissecting a series of the young of *Testudo horsfieldii*, I find that the very young (50 mm.) presents a bony network of costal and neural plates, modified ribs, and undeveloped plastron, similar to the young *T. loveridgii* (60 mm.). The two are compared in text-fig. 21. Series in other species, chosen at random, show the same thing, with, of course, variations. In some the dermal plates are more equalized, and in the early stages present a less net-like form, each costal being kite-shaped, rather as in the Turtles. In the Giant Tortoise (*T. nigrita*) from the Galapagos, a very young specimen (95 mm.) has the bony carapace still extensively fenestrated; the costal plates are more or less equally developed, each being dilated beneath the vertebro-costal sutures, and from thence narrowing to the marginal region, the fenestræ between are therefore equal. The neural plates are broadly developed; second, fourth, and sixth are not in contact with the corresponding costals. The general structure is therefore in essentials the same as in *T. loveridgii*. In Freshwater Tortoises, such as *Emys*, development is proportionately quicker beneath the vertebral shields, a specimen of 50 mm. having this part of the carapace entire, whilst the costal region is only half completed.

In the following section the development of the costal and neural plates will be dealt with further, in connection with their origin.



*Origin of the costal and neural plates.*

Much has been written on the origin of these plates, and many ingenious theories have been propounded\*.

Most authors agree that the marginals, nuchal, and pygals are of dermal origin, and that the plastron is derived from the sternum and gastralia which have become greatly modified, but the question of the neurals and costals is still unsettled.

The earliest opinion worth citing is that of Cuvier (1799), who considered that the costal plates were formed "par les dilatations de huit côtes ou bâtons osseux qui prennent naissance sur les unions des vertèbres, et se terminent à un rebord qui entourent toute la carapace." The idea that the plates are dilatations of the vertebral spinous processes and true ribs is held by many subsequent authors—Geoffroy St. Hilaire (1809), Bojanus (1819–21), Rathke (1848); or, further, that these plates originate in periosteal or differentiated tissue—Goette (1899), Haycraft (1899), Newman (1906). Haycraft (1891) formulates a theory that costal plates are rib-expansions formed where there is no differentiated periosteal membrane confining the rib. In the case of turtles, where the expansion does not reach the marginal, he states that the distal portions which preserve their rib-like form are unable to expand because "they are invested by a restraining periosteum." The fact that the costal plates in most Chelonians develop gradually towards the marginals, passing through the stage normal to adult turtles, disproves this theory.

Carus (1827) and Gegenbaur (1889) thought that the costal plates were greatly developed vertebral transverse processes—a view which, of course, is immediately disproved by the fact that their points of origin are distinct and widely separated from the vertebral column.

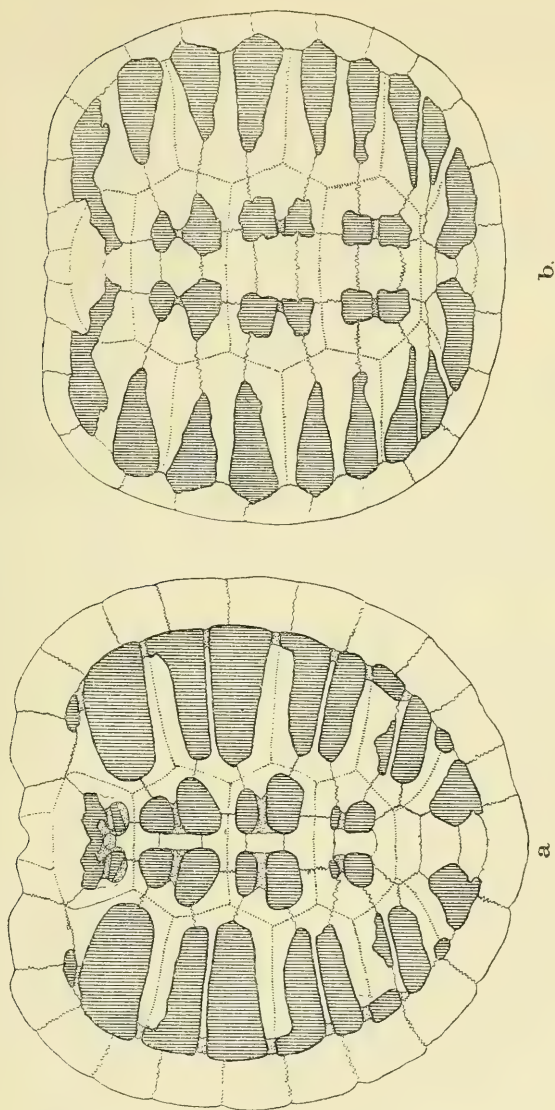
O. P. Hay (1901) accepts none of the foregoing theories. He distinguishes three layers of bone—dermal, fascial, and cartilaginous. The first is present in the armour of *Dermochelys*, the most primitive living Chelonian. The modern costal and neural plates are formed not by dermal but by the fascial bone, which since it is completely united to the cartilage elements, appears to arise directly from the perichondrium, as observed by Goette (1899).

That these plates are dermal in origin and similar in every way to the nuchal, pygal, and marginal plates was first suggested by Carus (1834), and was followed up by Peters (1838), Owen (1849), Baur (1887), Gadow (1899, 1905, 1909), and Versluys (1914). Many points brought to light in the present study corroborate this view. For instance, the fact that the true ribs are degenerating throughout their length by absorption within the periosteum whilst the costal plates are in process of actual development, and also the marked difference in the texture of

\* "Hypothesis follows hypothesis; the theoretical rubbish-heap accumulates; and truth ever eludes us."—FABRE (transl.).



Text-figure 21.



Young specimens of *T. loveridgii*, **a**, and *T. horsfieldii*, **b**, compared.  
 Epidermal shield-sutures .....; underlying rib :::::; fenestræ |||||.

the two forms of bone, seem to indicate that these are independent structures. It will also be remembered that in stripping the carapace from the young specimen of 42 mm., some of the neural plates adhered to the carapace rather than to the vertebra. Another point against endo-skeletal origin is the alternating level at which the costal plates arise on consecutive ribs, according to the arrangement of the epidermal shields above them.

This brings up the question, also unsettled, regarding the correlation of epidermal shields to the underlying plates. If the plates are of dermal or fascial (sub-dermal) origin, one presupposes such a correlation; if of endo-skeletal origin, there should be none. Various authors argue the case accordingly, H. H. Newman opposing any idea of correlation very strongly, whilst Gadow treats it as an accepted fact. G. H. Parker (1901), in his paper on the Sculptured Tortoise, attempts to explain the alternating arrangement of these two structures by applying Harrison's observations on the regenerating tail of a tadpole (1899). He says (p. 23):—"The tail of a developing tadpole is composed of an outer covering of ectoderm—which ultimately gives rise to the outer layers of the skin—and of a core of mesoderm. These two masses of tissue grow in very different ways, so that as the tail lengthens, the ectodermic covering, which is most actively produced anteriorly, slips posteriorly over the underlying mesoderm, whose region of growth is chiefly at the posterior end. Although this posterior migration of the ectoderm has been actually demonstrated only in the tadpole, there is reason to believe that it occurs in other vertebrates."

The present study points to a very marked and obvious correlation between shields and plates in *Testudo loveridgii*, which, having its carapace in what one might term an incipient stage of development, throws much light on the subject. A careful study of many species of *Testudo* and *Cinixys* during the period when the plates are developing, brings forth a wealth of evidence that this correlation is an indisputable fact in these genera. In newly-hatched individuals of *T. loveridgii* (and also those of *T. ibera*, *græca*, *horsfieldii*, *leithii*, etc., etc.) the bony plates are lacking beneath the areolars, developing apparently as the shields themselves commence to form their growth-rings. In specimens of different species the amount of plate which has accrued at the end of the season's growth varies, but is at first in all cases greater beneath shield-sutures (that is around the shield-edges) than elsewhere. The neural plates beneath a shield-suture are developed laterally, whilst the alternating ones are not. The costal plates beneath the costal shield-sutures are at least twice as broadly developed as those between; their proximal portions, however, alternate in breadth and narrowness inversely in strict accordance with the overlying shield-sutures. Moreover, in the male type-specimen the X-ray plate (*vide* Pl. III.) shows that the bony plates are in perfect harmony with the abnormal third vertebral

shield-sutures, and are thus adapted to support four instead of five vertebrae. This fact points to dermal origin of the plates, but is in opposition to Parker's theory of ectodermic migration in *Chelonia* (*à propos* of the tadpole's tail), in which he points out that "any early local disturbing influence that affected both scute- and plate-producing tissues would leave its trace in the adult in the form of a region of modified scutes posterior to a region of modified bony plates." At the same time, this does not alter the fact that the plates are adherent to the bones of the true skeleton, and are coincident with them regarding numbers etc. Yet development seems to be influenced and regulated chiefly by that of the overlying dermal areas corresponding to the epidermal shields. This is also seen in the Giant Tortoises known to have thin carapaces, such as *T. abingdonii*, *microphyes*, etc., in *T. calcaratus*, and in fossil forms such as the Pleistocene Marsh Tortoises, *T. vosmaeri* from Rodriguez and *T. indica* from Mauritius. In these the form of the plates is similar to that of *T. loveridgii*, the essential network beneath the shield-sutures being of thick bone standing out in relief from the thin bone, which fills in what would be fenestræ in the young or in *loveridgii*.

In ordinary adult tortoises in which the carapace is complete and of equal thickness, this cannot be appreciated, but in these it can be studied in the initial stages of plate-development.

The following quotation from Owen (1849, p. 161), whose paper I had not read at the time of my own observations, corroborates in every particular what I have found to be the case in so many species:—

"A strong argument for regarding the costal plates as dermal ossifications rather than processes or continuations of the endoskeletal elements, to which they are attached, may be drawn . . . from the period of their ossification, and their relative position to the ribs with which they are connate.

"In the embryo *Testudo indica*\* the uniformly slender pleurapophyses are ossified nearly throughout their whole length before the ossification of the costal plates, usually regarded as their expanded tubercle, commences; and the beginning of the superadded bone† is not at the same point in each rib, as might have been expected if it were the exogenous process called 'tubercle' of the rib. The costal plates are situated in the young *Testudo indica* alternately nearer to and farther from the head of the rib; and their presence seems to be determined rather by the angle of union of the superincumbent vertebral scutella with the lateral or costal scutella, than by the necessity for additional strength of the articulation of the ribs with the spine. Ossification commences at the point from which the three impressions radiate, and as this point is

\* [Probably *T. nigrita* or *elephantina*, *indica* Schn. being an extinct species.]

† "This period, in its relation to the development of the neural arches and pleurapophyses, corresponds precisely with that at which the dermal plates of the Crocodile begin to be ossified."

nearer the median line at the median apex of the costal scutellum than at the lateral apex of the vertebral scutellum, the resulting plates of bone are alternately further from or nearer to the middle line; and the first, third, and fifth costal plates have advanced along the proximal end of the rib so as to join the neural plates, whilst the second, fourth, and sixth costal plates leave a portion of the proximal end of the rib uncovered and crossing the space between the incipient costal plates and the neural plate. . . .

"When the partially ossified carapace of a young tortoise is dried, one cannot fail to be struck with the difference in the texture and external surface of the bones which unquestionably belong to the endo-skeletal vertebræ, and of those which, notwithstanding their connection with neural spines and pleurapophyses, are developed in the fibrous substance of the corium. These nascent 'neural' and 'costal plates' of the carapace have a granular exterior and a coarse spongy texture, whilst the neural arches and pleurapophyses are compact, smooth, and with a polished external surface: the part of the pleurapophyses which passes beneath and is attached to the under surface of the 'costal' plate (pls. i.-viii.), contrasts strikingly with that superimposed dermal ossification.

"The marginal plates present the same rough, coarse, granular character as the neural and costal plates . . . . their ossification has been governed by the presence of the marginal epidermal scutes, and, as in the case of the costal plates, by the points of junction of contiguous scutes; each marginal ossification is accordingly impressed by the lines indicating the junction of the marginal epidermal scutes with each other and, in the case of the middle ones, with the contiguous scutes of the plastron."

The whole of the foregoing evidence therefore points to the fact that the costal and neural plates are of dermal origin, not endo-skeletal; and are, in fact, similar in this respect to the nuchal, pygal, and marginal plates.

Further, the correlation between the epidermal shield-sutures and the plates beneath, observed independently in the present study and previously by Owen, suggests that their growth is also correlated.

The areas of dermis beneath each shield are well marked off from one another by a fold and an underlying groove in which the shield-edges are implanted. It is probable that these dermal areas grow in the same manner as their superimposed shields, and that the bony plates beneath, which are of dermal origin, have their growth similarly regulated.

The following hypothesis is therefore suggested:—

*That the bony plates of the carapace develop from the dermis, primarily in the areas of growth activity.*



(a) Where this takes place concentrically, as seen by such striations in the epidermal shields, the plates in the early stages of development are localised principally beneath the shield-sutures, as in *Testudo*, *Cinixys*, etc.

(b) Where growth is uniform throughout each area, development of the plates is also equalised, proceeding from the individual centres of ossification, as in *Emys* etc.

#### SUMMARY.

*Testudo loveridgii* has an excessively depressed soft-shelled carapace, and is able to inflate itself to a certain degree. It possesses a bony carapace and plastron, but they are extensively fenestrated, incomplete, and similar in essentials to the juvenile stages of other species.

Marginal plates five, six, and seven spread inwards in a unique manner, entering into the composition of the plastron and separating the hyo- and hypoplastrons from each other. Their upper portions are extraordinarily shallow.

The ribs in *T. loveridgii* become (usually) entirely absorbed, apparently by the osteoclasts which are present beneath the periosteum. A simulacrum of the capitular portion, soft like ligament, and formed chiefly of periosteum, persists for some while.

The neural arch is vestigial and sometimes completely wanting, the neural plates being applied to the depressed centra to form the roof of the neural canal. Absorption probably takes place to some extent as in the ribs, but the arch is never more than a simple layer of bone, without spinous processes.

The jaws, together with their investing horny sheaths, are denticulated with remarkable regularity.

*Fenestration in this and other species is caused by arrested development*, and not, as previously supposed, by absorption with age.

*The development of the bony plates in T. loveridgii and the young of other species points to the neurals and costals being of dermal origin.* The principal evidence is:—

(1) *That they are developing whilst the ribs and neural arches of the true skeleton are degenerating.* (2) *That the point of origin of each costal plate is alternately nearer to and further from the rib capitulum.* (3) *That the form of these plates in their early stages of development is in strict correlation with the borders of, or sutures between, the superincumbent epidermal shields.*

It seems possible that *the development of the plates is regulated by that of the areas of dermis corresponding to the epidermal shields*; (1) *forming a network as in T. loveridgii and other species when this growth proceeds concentrically*, or (2) *proceeding equally from each centre of origin where dermal growth takes place equally within each area as in Emys etc.*



## NOTES.

The following field-notes and observations on the original specimens, and those collected on subsequent expeditions, are contributed by Mr. Loveridge:—

*“Habitat.*

“The first specimen of this tortoise which I met with was found dead at the foot of a precipitous rock some 40 feet in height and situated near the top of a rocky kopje 500 feet above the surrounding dry thorn-bush country. From the flattened and broken remains, I concluded that it was a species unknown to me, and crushed by a rock having fallen upon it. (The rocks are grey granite, sheer precipices on the kopjes and rounded boulders scattered on the plains around. Most of the specimens have been collected beneath the latter.) On December 8th, 1918, my native collector brought in a small specimen which I at once assumed was *T. tornieri* Sieb., of which I had read brief notices but had never seen the original description. During succeeding days two batches of these tortoises were found in crevices or beneath rocks, but though I did not leave the district till December 28th, and had a native looking for them constantly, no more were found.

“On January 1st, 1921, I sent the same boy who was with me for two years before, back to the same locality which lies south of Dodoma in arid country. Here, again, he found but two or three specimens, but, ranging round, came upon another kopje where they were more plentiful, though he alleged that without a single exception they were under the rocks, of which he had to remove a great many before being able to effect captures. He had one piece of good fortune in finding four young specimens all together beneath one boulder, with the exception of a slightly larger one already caught; these were the only young specimens taken. The smallest of these was unfortunately trodden upon and promptly died. The shell is much depressed as in the adult. When Mr. Boulenger described the species in 1920, he assumed a small dome-shaped tortoise, which I found preserved in a bottle (no data) in a German house near Morogoro, to be the young of *T. loveridgii*; this, however, is disproved by the finding of young specimens with depressed shells.

“In November 1921, I spent an afternoon with my boy looking for *T. loveridgii* at Dodoma. He first took me to the place where he got the eleven tortoises, which is not on a kopje but on a huge rock 100 yards from a kopje. The rock is about 30 feet long and 10 feet wide, and slopes up from the ground to a height of 7 or 8 feet. On the knob is a flattish boulder, and beneath this he found them all in January (evidently aestivating—January and February being our hottest months). The tortoises therefore climbed up the boulder: one would certainly never think of looking for them in such a spot. We then went to the place where he

found the three—in a cleft of a split boulder; they had to climb the boulder and slide down an almost vertical cleft, where one would suppose they could not get out; the cleft was about 18 inches. In this cleft, amongst a litter of dead leaves, were two not half-grown individuals. We hunted about all the rest of the day, but found no more. . . . Their markings are very fine; Tabora specimens are noticeably darker than the Dodoma ones.

“*Pairing.*

“On December 12th, 1921, at 4.30 P.M., I observed two specimens paired for the first time. A native said they had been so approximately for half-an-hour. The shell of the male formed an angle of 45° with that of the female; his fore-feet were in the air; he kept moving his head in and out of his shell and had his mouth wide open. In April this female and others were heavy with eggs. On January 13th two more tortoises were paired at 9 or 10 A.M. and from that date and onwards pairing took place daily, usually between 9 or 10 A.M. and 2 P.M. The female generally walked away with the male following; frequently the latter became impatient and snapped at her limbs, or crawled on her back, making vicious snaps at her head whenever it appeared. On a couple of occasions the males were so ill-tempered that they seized the edges of the females' shells in their jaws and dragged them along, finally getting beneath them and apparently endeavouring to overturn them.

“*Habits of T. loveridgii compared with those of Cinixys belliana.*

“As I had these species under observation for four months confined in the same enclosure, I found it very interesting to compare the habits of an exceptionally highly-specialised Box Tortoise with those of a retrogressive and soft-shelled species.

“Owing to neither my native collector nor myself finding *T. loveridgii* in the open, I had come to the conclusion that it was nocturnal; with a view definitely to ascertain if this were indeed so, I visited the enclosure at all hours of the night up to 1 A.M., but with one or two solitary exceptions never found them out. At dusk they always retired beneath the heaps of stones and boulders provided for them, and there they piled themselves up, one atop of another, a great deal of noise being caused by the scratching of claws on shells. They did not again make an appearance until several hours after daybreak, which varied according to the dullness or brightness of the morning.

“*C. belliana*, on the other hand, not infrequently stayed out at night, and particularly when rainy; all seven of them would spend the night in trying to escape from the enclosure. Moreover, *C. belliana* was always on the move at daybreak. On further reflection it was obvious that in their soft shells *T. loveridgii* would fall an easy prey to the carnivores roaming about after nightfall, and which are very plentiful in the Dodoma district

(Leopard, Ratel, Civet, Mongoose). This was brought home to me very forcibly one night by a Civet entering an adjoining enclosure and eating four and a half young crocodiles in one night. The shell of *C. belliana* would resist most attacks; the thickness of their bony defence as seen in a sawn-through section is astonishing.

"*T. loveridgii* shows a fondness for climbing up and falling off the rockeries of its enclosure, which pastime, indulged in in its natural habitat, calls for a rapid recovery in turning over; it also displays great agility in climbing up wire netting. One day eight specimens of the Soft Tortoise succeeded in escaping through a hole in the wire netting; two were recovered in three days, being found on the second and third days at some huts 400 yards from the hill. They appear to feed oftener than *C. belliana* and are quite voracious. They feed well on a succulent grass here; the previous specimens taken home were fed on lettuce, and when this failed were induced to eat bread soaked in jam. *T. loveridgii* generally retires to its retreat when a shower comes on, but on occasion I have known the whole lot turn out during heavy rain and feed voraciously, probably being thirsty.

"I was at first disposed to think that *T. loveridgii* could not swim, as the first half-dozen arrivals on being placed in water sank to the bottom of the bath and remained there without putting forth any effort. On seeing some young ones struggling in water and trying to swim, I retrieved a couple of females, which struck out well and kept themselves up when placed in a bowl of water."

Unfortunately nearly half of these valuable tortoises, kept alive by Mr. Loveridge, succeeded in escaping, several doing so *en route* to the coast on their way to me. Several spirit specimens also came to grief, but a sufficient number remain, reinforced by still later collections, including a beautiful series of young, to enable a thorough study of this most variable species to be made.

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## EXPLANATION OF THE PLATES.

PLATE I. *Testudo loveridgii* Blgr. ( $\frac{3}{4}$  nat. size).

PLATE II. Radiograph of ♀ type-specimen (nat. size). Showing correlation between bony plates and epidermal shield-sutures (visible as a network of white lines).

PLATE III. Radiograph of ♂ type-specimen (nat. size). Showing correlated shield and plate abnormalities.



27. Notes on the Anatomy of *Cacopus systoma*, an Indian Toad of the Family Engystomatidæ. By D. W. DEVANESEN, M.A.\*

[Received April 4, 1922 : Read May 9, 1922.]

(Text-figures 1-19.)

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1. *Introduction.*

*Cacopus systoma* is an Indian toad of the narrow-mouthed, edentulous and fossorial type belonging to the family Engystomatidæ, well-known for their habit of feeding upon ants and termites. Among the chief characters which distinguish the genus are the following: the palate has two dermal transverse folds more or less denticulated, one behind the vomers and the other in front of the œsophagus; there are no pre-coracoids; the sternum is a large cartilaginous plate; and the transverse processes of the sacral vertebra are rather strongly dilated.

The following notes were compiled in India during what was intended to be a comprehensive study of the morphology of *Cacopus systoma*. Comparisons with the anatomy of certain other toads of the same family and comments thereon have been made wherever suitable.

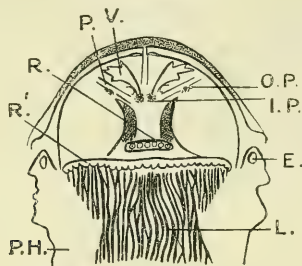
This work was done in the Zoological Laboratory of the Madras Christian College, Madras. Grateful acknowledgment is hereby made for suggestions and advice to Prof. W. Rae Sheriffs of the college mentioned, and to Dr. J. R. Henderson, F.L.S., formerly Superintendent of the Government Museum, Madras. To Prof. MacBride's encouragement the communication of this paper is due; for this and for reading the manuscript, I thank him.

\* Communicated by Prof. E. W. MACBRIDE, D.Sc., LL.D., F.R.S., F.Z.S.

## 2. The Viscera.

The second dermal ridge on the palate of this toad is a conspicuous structure stretching across from one eustachian opening to the other, its edge being thrown into well-marked denticulations. On laying open the pharynx\*, one finds immediately behind this ridge and in close contact with it and occupying more or less the same level, a differentiated area of about 80 sq. mm. (text-fig. 1). Transverse sections through the same revealed the fact that it consisted of closely-set, parallel, and longitudinal reduplications of the mucous membrane of the pharynx, each fold containing an extension of the basement membrane (text-fig. 2). A fold is on an average 1 mm. in height; the highest folds are found in the middle, and from this place the height of the folds on the sides gradually decreases. These

Text-figure 1.



"The Pharyngeal Organ of *Cacopus systoma*" exposed; the lower jaw and the floor of the mouth have been cut away. L., lamellæ arranged lengthwise; R., the first, short, R', the second, long, denticulated ridge; E., eustachian opening; V., vomer; I.P., inner dark papilla on the toothless hind end of a vomer (V.); O.P., an outer one on the vestigial palatine (P.); P.H., pharynx cut open and deflected.

folds show a faint tendency to anastomose, and their free edges hanging down into the cavity of the pharynx, in the fresh condition, appear swollen. This specialised area of the pharynx may, in my opinion, be given the status of an organ for two reasons: first, it is compact, having a certain definite outline, and it is restricted to a definite place, namely immediately behind the second dermal ridge; secondly, as the free end of the tongue lies, when in a state of rest, underneath this area, and since the presence of the intermaxillary glands is doubtful in this toad, the structure in question is probably a substitute for these glands, possessing a similar function; the cells of the mucous membrane in these folds are comparatively large and sacciform, which facts are perhaps suggestive of their glandular nature.

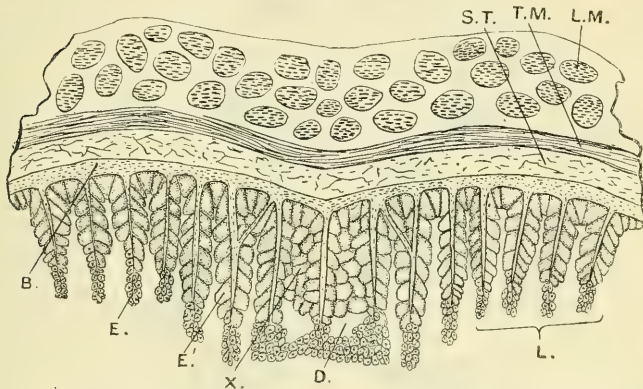
\* That part of the alimentary canal between the second dermal ridge and the stomach, I propose to call "the pharynx," as it is much wider than it should be for an œsophagus which is probably unrepresented in this toad. The cavity enclosed between this ridge and the jaws may be termed "the oral cavity."

I therefore propose to call this the "pharyngeal organ" of *Cacopus systoma*. It will be interesting to know if this structure is present in the other members of the family Engystomatidæ.

On the outer surface of the pharynx, from each of the two points roughly corresponding to the two ends of the second dermal ridge, is given off a slip of tissue which is attached to the free end of that arm of the pterygoid meeting the cranium. This arrangement is presumably for the purpose of holding up the pharyngeal wall which, in this region, is particularly heavy with the dermal ridges and the "pharyngeal organ" described.

The longitudinal folds of the mucous membrane of the stomach appear to be more numerous than in *Rana*, and in the convex region thereof they show a tendency to anastomose. The liver

Text-figure 2.



A transverse section through the middle region of "the pharyngeal organ."

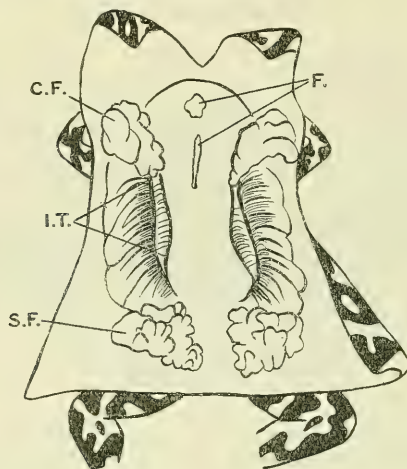
L.M., outer lengthwise muscles of the pharynx; T.M., inner transverse ones of the same; S.T., sub-connective tissue; B., basement membrane; L., lamellæ; E., ordinary stratified epithelial cells; E.', the same epithelial cells enlarged and forming a sac; X., cell-mass resulting from the fusion of two adjacent lamellæ; D., an incipient duct.

consists of but two lobes. Among the numerous specimens I examined, I found eight—six females and two males—suffering from stone in the bladder. The proximal part of each oviduct where it opens into the cloaca becomes enormously dilated into a sac, which may be distinguished as a uterus. In this bag probably the eggs are stored before they are finally passed out. It consists of a thick-walled, less capacious anterior portion and a membranous spacious posterior part. The internal lining of the former is thrown into numerous, densely-packed, villi-like processes, visible to the naked eye. The two bags or uteri are, along their inner sides, intimately connected by tissue; I do not think that there is an actual fusion between their walls. The kidney possesses a simple lobe towards the hind inner end.

### 3. *The Sub-cutaneous and other Fat-bodies\**.

The occurrence of sub-dermal fat is by no means peculiar to this toad; several species among the Anura are known to possess it, though its function in most of them still remains to be elucidated (Boulenger, C. L., 3). Accumulations of the fat in question are found in *C. systoma* chiefly in two situations: (1) in the neck-region above and below, in connection with the lymphatic maxillary septum; this lobular mass of fat may be termed "the cervical fat-body" (text-figs. 3 and 13); and (2) in the inguinal region on the dorsal surface in relation with the lymphatic inguinal septum, which is very high and falls into folds; in the

Text-figure 3.



The skin on the back cut open and the sub-cutaneous fat-bodies exposed in a male  
 C.F., cervical fat-body; S.F., supra-inguinal fat-body; F, fatty deposits on the head and neck; I.I., conspicuous *inscriptions tendinæ* of the *obliquus* muscles, seen only among males.

same region, but to a less extent, fat is developed in connection with the iliac sac and the posterior lymph-heart; this extensive area of fat, in its totality, may be called "the supra-inguinal fat-body" (text-fig. 3). Besides these two conspicuous sub-dermal fat-bodies, one occasionally finds scanty deposits of the same substance under the skin in the parietal and occipital regions, in a small median area dorsally behind the head and on the under side of each arm near the brachial vein. I assume that these, too, are developed in relation to the lymphatic system.

One also finds in this toad certain internal deposits of fat

\* Young specimens show neither an adequate development of these fat-bodies nor are they present in all the places mentioned.



which presumably are sub-peritoneal fat. These are found in relation to the blood-vascular system and the vertebral column. The auricles and the *truncus arteriosus* are thickly covered with fat, and the ventro-auricular groove is filled with the same; this cardiac fat, it should be observed, is found on the inner layer of the pericardium. Small quantities of fat occur also on the walls of the *inferior vena cava*, where it opens into the *sinus venosus*. In close proximity to the vertebral column is situated a longitudinal patch of fat on both sides extending from the fourth vertebra to the ninth, and a small median deposit where the cranium articulates with the atlas.

Among the other Indian frogs I examined, sub-dermal as well as sub-peritoneal fat in relation with the blood-vascular system was found in *Rana hexadactyla*, the analogous form in India to *Rana esculenta*, and in *Rana breviceps*, a burrowing species. Nevertheless, in these instances, while fat under the skin is confined to the neck-region, even that does not occur so regularly. The same fat in the inguinal region has been noticed by other observers in several species of *Bufo* (3), *Xenopus laevis*, and notably in *Hemisus guttatum*, an American Engystomatid (1); in the first-mentioned toad, however, it is ventrally situated, while in the last one there is a complicated development of the same in connection with the iliac sac which does not obtain in *C. systoma*.

As this Indian toad has a remarkable habit of burrowing underground when the dry-season commenced and of passing into a torpid state, it struck me that these fat-bodies might have a nutritive value to the animal during that æstivating period. Therefore, in July and August, 1911 and 1912, I obtained by special efforts a considerable number and examined them. It was found that both the sub-dermal and sub-peritoneal fat-bodies had undergone, in accordance with my expectations, a great reduction in size and a change in colour from yellow to dull white, as compared with specimens examined during the wet-season.

From the above considerations one may draw the following conclusions:—Fat occurs normally in several places in the body of *C. systoma*, both internally and under the skin. While the pre-renal fat-bodies may be looked upon as feeders to the gonads during the breeding season, the other fat-bodies in this toad may be regarded as assisting in the general nutrition of the body during æstivation. It is noteworthy that in *Bufo*, *Hemisus*, and this toad the sub-dermal fat is developed in connection with the lymphatic system.

#### 4. Discussion on "the stout shape"\* of *C. systoma*.

A remarkable feature of the two toads of this genus is, as several observers have noted, the rotund shape of the body. This has been, till now, accounted for in various ways. Thus, Günther (6)

\* Vide figure in Boulenger, G. A. (2), p. 496.



observed regarding *C. globulosus* that it was due to a certain fluid contained in the abdominal cavity and the extraordinary development of the ovaries in the female. But Pearson (7) remarks as follows:—"Günther states that this distension is caused by a fluid contained in the abdominal cavity. A brief examination shows that this is not the case, and that the fluid-containing cavity is none other than the sub-cutaneous lymph-sinuses which are greatly enlarged in this form. The dorsal sinus is especially spacious, and has a height of 15 mm. from floor to roof. (The length of the frog from mouth to vent is 75 mm.)"

"In Günther's account he speaks of the distension of a female specimen being due to the growth of the ovaries, and his description suggests that the ovaries grow into the large cavity on the back. This is not possible, as the sub-cutaneous lymph-sinuses are separate from the coelom. There is only one other species in this genus, namely *Cacopus systoma*, which differs but slightly from *C. globulosus*, and which resembles it in the robust appearance due to the enlargement of the sub-cutaneous lymph-sinuses. This interesting character is not given in the diagnosis of the genus either by Günther or Boulenger."

Thurston (8), with reference to the same species, says:—"On laying open the visceral cavity, the globular shape was found to be due to an enormous distension of the oesophagus and stomach, the latter occupying nearly the whole of the abdominal cavity, and the remaining viscera &c. being compressed and lying posteriorly. There was no distension of the intestinal tract. The distension of the oesophagus and stomach was found on section to be caused by the presence in their cavities of a mass of winged white ants (termites) which when dried weighed 326 grains."

The descriptions of Günther are based on slender evidence, namely the examination of two specimens in spirit. So far as I was able to observe in several fresh specimens of *C. systoma*, I did not find an excessive quantity of the peritoneal fluid beyond what should generally be expected in the abdominal cavity. The supposition that the development of the ovaries is a source of the stoutness may at once be dismissed, as it can apply only to females, and again in them it is seasonal as in all batrachians. So also Thurston's hypothesis, as food cannot be regarded as a permanent cause.

I find that the stout shape of the body in this toad cannot be accounted for by any one character, but by a combination of features as the following:—The viscera as a whole exhibit a great development which is disproportionate to the small dimensions of the abdominal cavity. They therefore press against the sides of the abdomen and bring about a characteristic rotundity of the same. A feature which has not been noted as regards this toad is the inclusion of the proximal portion of the thigh into the trunk. The skin of the thigh is drawn along with that of the body, and consequently the contour of the latter

begins posteriorly about the middle of the thighs\*. This, I should think, improves upon the effect produced by the viscera. The enlarged lymph-sinuses, with the lymph and fat-bodies contained therein, enhance the stout shape.

The purpose of the enlarged lymph-spaces of the two toads of this genus is perhaps to be sought in their fossorial habits. The liberally secreted lymph may serve to protect the internal organs from injuries incidental to animals with such habits. The muscles of the abdomen in *C. systoma*, chiefly the *rectus abdominis*, form a weak protection, as they are stretched to their utmost capacity by the pressure of the enormously-developed viscera. The presence of a fluid between the latter and the skin must, under such circumstances, serve to diminish the chances of injury from outside. This supposition is strengthened by the fact that larger quantities of lymph were found in specimens obtained during the dry weather than in those examined during the wet-season.

### 5. The Axial Skeleton.

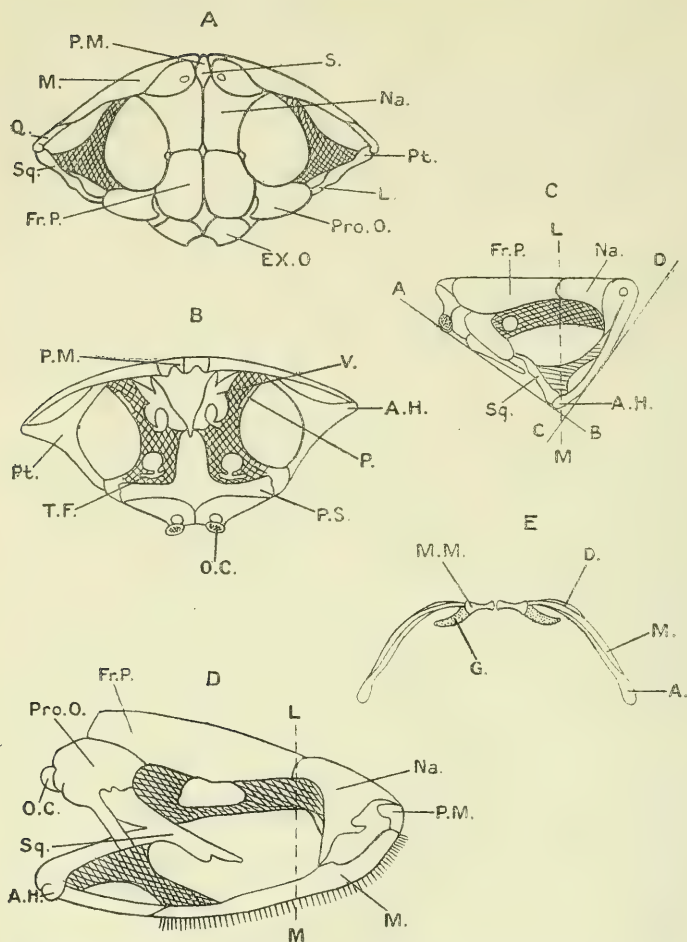
An examination of the bones of the head revealed certain facts which, in my opinion, account for the narrow mouth of this toad in particular, and probably also for that of several other members of the same family in general. While the contour of the mouth which corresponds to the distal circumference of the skull, is a parabola in *Rana*, the same has been in this animal reduced to a mere arc. Assuming that the skull-morphology in *Rana* is primitive, one can trace the narrow mouth in question to a generally vestigial condition of most of the bones of the suspensorium. Thus the squamosal has lost the anterior arm or the zygomatic process, what remains probably corresponding to the middle† and posterior arms of the same in *Rana* (text-fig. 4 A). The palatine, for another instance, is so inconspicuous, being about 3 mm. long, that it can only be found in skulls very carefully prepared. The remaining bones of the suspensorium also exhibit in a greater or a lesser degree the same degenerate state; the cumulative effect of this, in all probability, was the forward displacement of the articular head for the lower jaw. For, a line drawn along the suture between the nasals and the frontoparietals cuts the orbital fossæ at about the middle and passes through the heads in question (text-fig. 4 C), whereas in *Rana* the same line lies far in front of the last (text-fig. 4 D). This shifting of the articular heads necessitated by the vestigial condition of the bones of the jaws has probably led to a diminution in the contour of the mouth.

The cranium as a whole is remarkable for its shortness and

\* This character is greatly exaggerated in *C. globulosus*, judging by the specimen in the Government Museum, Madras. Beddard (1) has recorded a similar condition, still more pronounced in *Breviceps verrucosus*, an Ethiopian Engystomatid.

† The presence of this middle arm is also doubtful, as the attachment with the pro-otic is by means of a ligament which may, however, be taken to represent this arm.

## Text-figure 4 (A, B, C, D, and E).

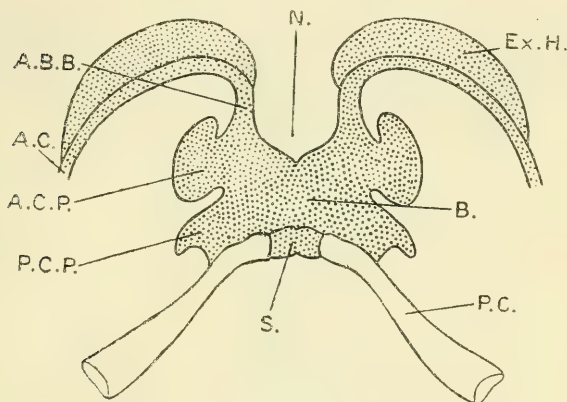


- A.** A dorsal view of the skull of *Cacopus systoma*. The vestigial condition of the squamosal (Sq.) is remarkable. L., ligament connecting the latter with the pro-otic. For other letters consult the key-list of abbreviations.
- B.** A ventral view of the same. P., vestigial palatine; T.F., trigeminal slit. For other letters consult the previous text-fig. (A) and the key-list of abbreviations.
- C.** A lateral view of the same. L-M., a straight line drawn along the suture between the nasals and the fronto-parietals of the cranium. A-B, the plane in which the proximal circumference of the skull lies. C-D, the plane in which the distal one of the same lies. A.H., articular knob for the lower jaw; Fr.P., fronto-parietals; Na., nasals.
- D.** A lateral view of the skull of *Rana hexadactyla*. A brief comparison of the *Cacopus* skull with this will reveal the differences mentioned in the text. L-M., the same vertical line mentioned in the previous text-fig. (C). For other letters consult key-list.
- E.** Lower jaw of *Cacopus systoma*, as seen from below. A., angulosplenial; M., Meckel's cartilage; D., dentary; M.M., mentomeckelian; C., cartilaginous portion of the latter.

relatively greater width, this being mainly due to the splenethmoid, which is extremely short, and it does not exhibit the prismatic shape usually seen in that of *Rana*. Each mentomeckelian of the lower jaw carries at its posterior end a cartilaginous triangular piece which stretches behind and is free from the other component parts of the same jaw. These two pieces are useful in so far as they provide partial attachments to the *sub-mentalis* muscle below and the *genioglossus* above (text-fig. 4 E).

The semilunar piece of cartilage in connection with the anterior cornua of the hyoid bone in *Hemisus*, described and identified

Text-figure 5.



The hyoid skeleton of *Cacopus systoma* viewed from below. Ex.H., "extra-hyal"

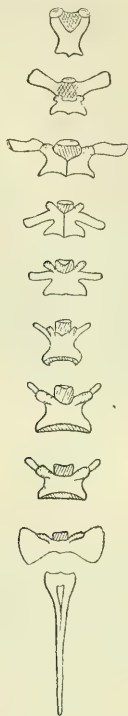
A.C., anterior cornu; P.C., posterior cornu; B., basihyal or the hyoid plate; A.C.P., anterior cartilaginous process of the basihyal; P.C.P., posterior one of the same; A.B.B., anterior body-process of the basihyal or the proximal part of an anterior cornu; N., notch between the latter; S., thick cartilaginous part between the proximal ends of the two posterior cornua, probably belonging to the latter.

as "the extrahyal" by Beddard (1, p. 909), appears to be represented also in this toad (text-fig. 5, Ex.H.). A closer approximation and fusion of the two extrahyals would complete the notch into a foramen corresponding to that of *Hemisus*.

In the vertebral column of this toad one finds also a few interesting features. The transverse processes are comparatively short, taking the size of the centra and the neural arches into consideration; those of the third vertebra are the longest; next in order follow the ninth, fourth, second, eighth, seventh, sixth, and the fifth; the last three may be subequal. The spinous processes may be said to be absent in the first, sixth, seventh, eighth, and the ninth vertebra, while in the rest it is probably represented by a faint median ridge. The thick transverse processes of the second, third, and the fourth vertebra, the thin

and slender ones of the fifth, sixth, seventh, and the eighth vertebra (those of the last three being directed conspicuously forward), the much dilated one of the sacrum, and the crestless urostyle combine to give a characteristic appearance to the vertebral column of this toad (text-fig. 6). It may be mentioned that the sacral diapophyses are remarkable for their uncommonly well-developed epiphysial cartilage at their free edges.

Text-figure 6.



A dorsal view of the bones of the vertebral column of *Cacopus systema*.

I noticed an interesting abnormality in one specimen, namely the occurrence of two sacral vertebrae, the posterior one being fused with the urostyle. This condition is found normally to exist in *Pelobates*, *Pipa*, and *Hymenochirus* (5, p. 22).

#### 6. *The Appendicular Skeleton.*

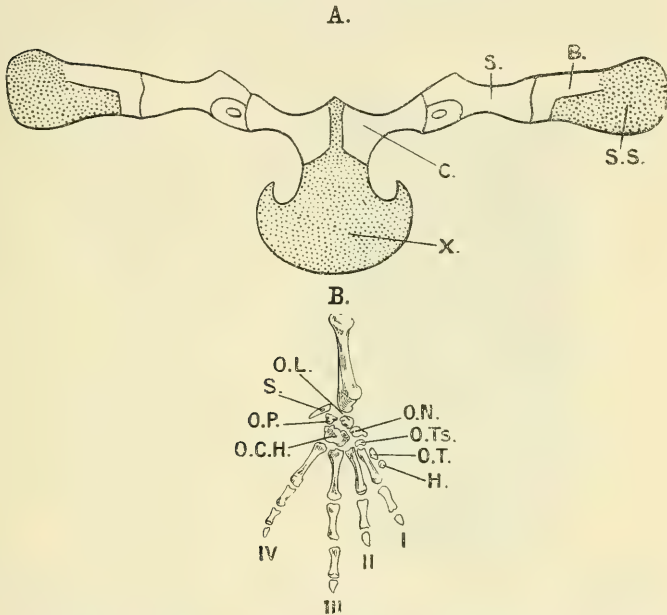
In the pectoral girdle the absence of the precoracoid probably necessitated the disappearance of the omosternum and the episternum. In the place of the sternum proper and the xiphisternum, one finds a broad, flat plate of cartilage generally calcified in the centre. This plate gives attachment to four different



muscles, viz., the *obliquus-internus*, the inner portion of the *sternohyoideus*, "*sternocornuoides*," and the "*abdominis-sternalis*," the last three to be described later in the section on muscles. This probably accounts for the unusually large size of this xiphisternal plate (text-fig. 7 A).

The "crista medialis," a ridge of the humerus which, according to Ecker (4, p. 42), occurs among the males of three European species of *Rana* as a sexual difference, is not to be found in the males either of *R. hexadactyla* or of *C. systoma*. The wrist-bones of the latter show greater calcification than those of

Text-figure 7 (A and B).



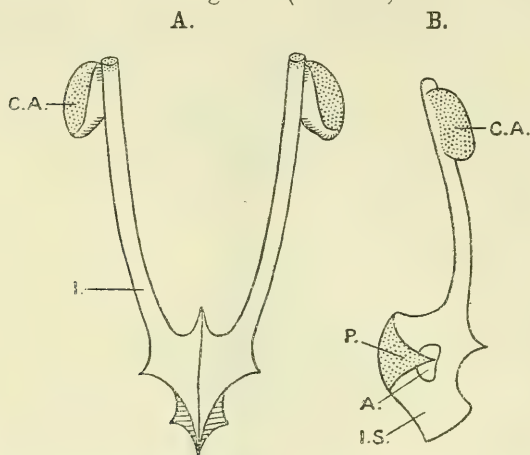
- A. The pectoral girdle of *Cacopus systoma*. X., xiphisternum; C., coracoid; S., scapula; S.S., suprascapula; B., an apparently bony portion of the latter.  
 B. The bones of a manus of *Cacopus systoma*. S., a sesamoid bone situated in a tendon; H., vestigial first finger. For other letters consult the key-list of abbreviations.

*Rana*; they also exhibit certain differences in their shape and in the details of their articulation with one another. In addition to the three bones of the proximal row mentioned by Ecker, one very often finds a fourth bone, which is exceedingly small, situated above and between the os pyramidale and the os lunatum. This may be a sesamoid bone, as it is placed in the course of a tendon (text-fig. 7 B).

In the pelvic girdle the absence of the iliac crest is remarkable when one finds that none of those muscles connected with the same crest in *Rana* is absent. Whether this crestless condition

of the ilia as well as that of the urostyle denotes a primitive feature, or whether it is a sign of degeneration, cannot be easily settled for the reason indicated above. At the free anterior end of each ilium there is found, attached to its outer side, a peculiar cartilaginous appendage. This has the shape of a plate, which, by folding on itself, encloses a groove into which is received the cartilaginous free edge of a sacral diapophysis. Thus the sacrum movably articulates with the ilium (text-figs. 8 & 10). In other words, the pelvic girdle, by means of the ilia, forms a gliding joint with the backbone through the sacrum. On the contrary, the sacral transverse processes in *Rana* are immovably attached by tissue to the anterior ends of the ilia, and consequently no movement in the manner mentioned above could take place. I was able to observe in emaciated specimens the ilia moving

Text-figure 8 (A and B).



A. The pelvic girdle of *Cacopus systoma* viewed from above. I., ilium; C.A., cartilaginous appendage of the latter.

B. The same girdle seen sideways. P., pubis; I.S., ischium; A., acetabulum.

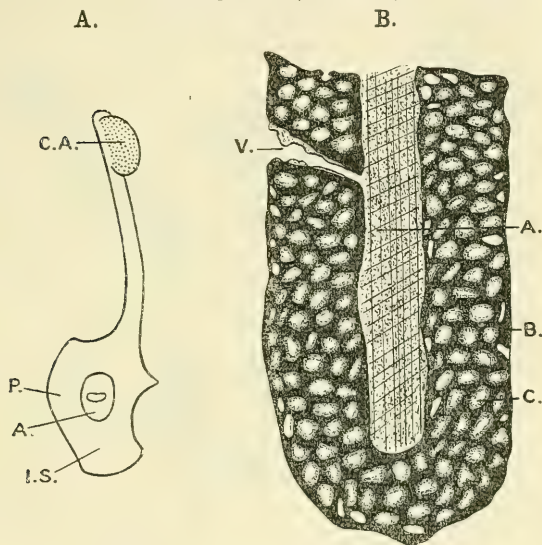
obliquely backward and forward during the act of burrowing. I should therefore suppose that this gliding joint has something to do with the same habit of burrowing.

Beddard (1, p. 12); with reference to a cartilaginous plate unconnected with the ilium but covering the sacral diapophyses in *Breviceps verrucosus*, remarks as follows:—"I imagine that this cartilage belongs to the ilium, and that it is in consequence related to it as the suprascapula is to the scapula. We have, in fact, in this frog an exaggeration of the grooving which the anterior end of other forms shows at its line of articulation with the sacral vertebra. It is, moreover, interesting to observe that we find in this frog a kind of foreshadowing of the relations which the ilia bear to the sacrum in the higher Sauropsida,

especially birds where the ilia are not merely attached to but cover the sacral vertebræ." In this Indian toad, however, the cartilaginous appendage in question not only covers the epiphysis of a sacral transverse process, but is also attached to an ilium. From the outer surface of the same appendage arises the *ilio-lumbaris*, a muscle which in *Rana* starts from the distal end of the ilium. These facts probably indicate that it really belongs to the latter, in which case the remarks quoted above may be, with less diffidence, applied also to the same ilio-sacral relation in *Cacopus*.

The pubis is interesting, as it exhibits signs of ossification

Text-figure 9 (A and B).



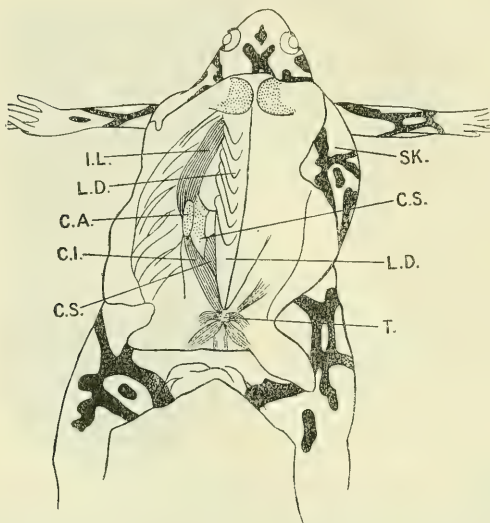
- A. A side view of the three bones of the pelvic girdle of an old adult *Cacopus*. It will be seen that the boundary of the pubis is indistinguishable; letters as in text-fig. 8 (A and B).
- B. A transverse section through the same pubis which suggested ossification. A., mass of degenerate cartilage at the symphysis; B., supposed network of bony tissue; C., degenerating cartilaginous matrix; V., probably a passage for a blood-vessel.

which, if real, would be another anticipation of what occurs normally among the higher vertebrata. In older specimens the ilium and the ischium appear to gradually encroach upon it till, at last, in very old ones, it becomes indistinguishable from either of them, both in its area and in its appearance (text-fig. 9 A and B). This suggests that, while there may be an ossification of the same, it has no separate centre, and that the process of substitution progresses from the adjacent boundaries of the ilium and the ischium. Sections through such a pubis after decalcification with picric acid show a structure which may be interpreted as an

incipient stage in ossification by substitution (text-fig. 9 B). No cartilage cell could be seen. The Haversian system may not be expected, as the pubis, if at all ossified, is more likely to become a spongy or cancellated bone. A median translucent mass (A.) found at the symphysis, I presume is a residue of the decaying cartilage not yet replaced. In this connection, I may mention that a similar phenomenon has been noticed in another toad, namely *Pelobates* (Gadow, p. 27).

Among the bones of the hind-limb, the femur, the "os naviculare," and the prehallux deserve attention. There is, on the ventral side of the femur, a distinct crest stretching from the middle to the anterior end, stopping short of the head of the same. It is from this "femoral crest" that the vastus internus

Text-figure 10.



A dorsal view of the ilio-sacral joint and a few muscles connected with the same.

For lettering consult the key-list of abbreviations.

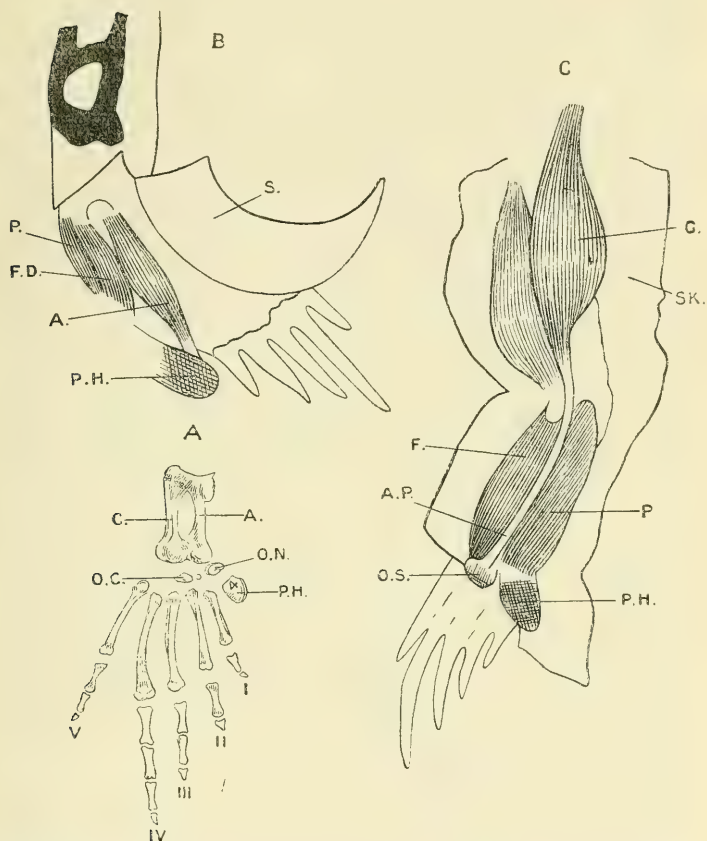
muscle arises. To this crest is also attached a considerable number of fibres of the *adductor longus*, *adductor brevis*, and the *pectineus* (text-fig. 19 B and C).

The os naviculare in the tarsus of this toad is a circular disc, convex in front and concave behind, and articulating exclusively with the astragalus. In front it is bound by tissue, and articulates as well with a certain piece of highly calcified cartilage which, as will be seen presently, is homologous with the prehallux of *Rana*. Though the tarsal bone in question has become so closely associated with the prehallux as to look like one of the component pieces of the latter, yet its identity could be recog-

nised with certainty by its connection with the muscle *adductor longus digiti I* (Ecker, p. 109; & text-fig. 11 A).

On the plantar surface of the foot in several forms of the Anura,

Text-figure 11 (A, B, and C).



- A. The bones of a pes of *Cacopus systoma*. P.H., prehallux; O.N., os naviculare; A., astragalus; C., calcaneum; O.C., os cuboideum.
- B. A side view of a pes of *Cacopus*, showing the relation of the muscle *abductor hallucis* A. to the prehallux P.H. P., *plantaris*; F.D., *flexor digitorum*; III, IV, and V, *longus*; S., skin cut and deflected upward.
- C. The skin (Sk.) on the plantar surface of the same, cut and deflected sideways in order to expose the muscles connected with the tubercles in question. G., *gastrocnemius*, showing its relation to the "os sesamoide" (o.s.) or the outer metatarsal tubercle; P., *plantaris*-inserted by means of a fascia on to the prehallux (P.H.) or the inner metatarsal tubercle.

particularly in those with a fossorial habit, has been observed a certain prominent tubercle of a horny consistency. It would



appear that till now this has been generally regarded as a cutaneous structure, rendered hard and horny in consequence of the nature of its function which is the scooping-out of the soil in suitable localities. This Indian toad has two such conspicuous tubercles, called by Boulenger (2) the "inner metatarsal tubercle" and the "outer metatarsal tubercle." On maceration, it was found that not only these were not purely cutaneous developments, but also that they had their counterparts in *Rana*.

It is a well-known fact that the Anura possess, in addition to the five toes normally present, an extra vestigial digit—the prehallux. Among the Indian frogs I examined, this digit consisted of four cartilaginous pieces in *Rana hexadactyla*, of two pieces in *Rana tigrina*, and of a single piece in *Rana breviceps* and *Cacopus systoma*. The first-mentioned frog is entirely aquatic in habit, and its prehallux forms a slight projection covered with ordinary skin, while in the three last-mentioned ones, which are burrowing forms, the same prehallux is converted into a conspicuous shovel-shaped organ enclosed in a hard and horny dermal sheath (text-figs. 11 A & 12 A, B, and C). The so-called "inner metatarsal tubercle" of *C. systoma* is therefore none other than the distal piece of the vestigial toe of *Rana* which has acquired a large size and a shape suitable for its function in this toad. That this is so was confirmed by an examination of its connection with a muscle, viz. the *abductor hallucis*, which is inserted on to the prehallux—a muscular relation identical with what obtains in *Rana* (Ecker, p. 109).

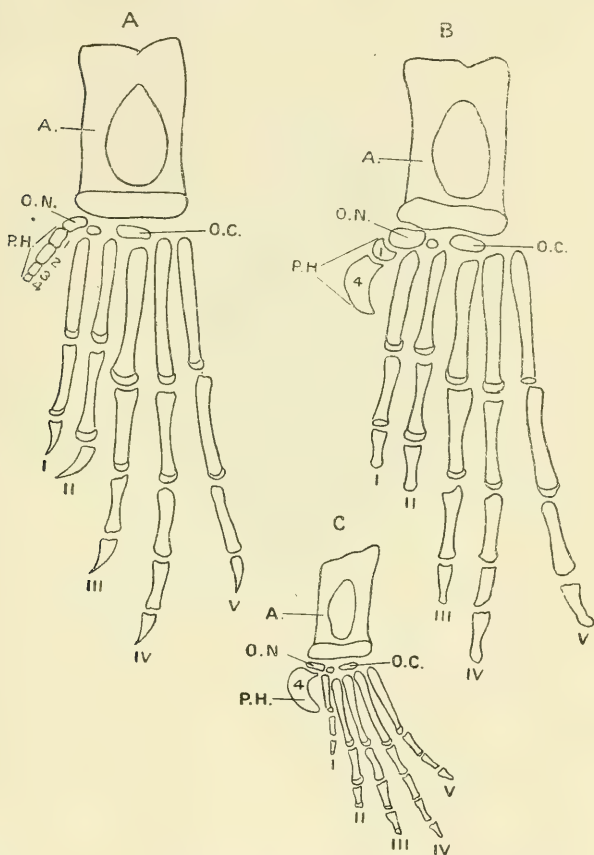
In the two terrestrial species of *Rana* just mentioned, one finds a gradual reduction in the number of pieces constituting the prehallux, assuming the condition in *R. hexadactyla* to be the normal one. Simultaneously with this reduction, it would appear that in these forms there has been an increase in the size and a change in the shape of the distal piece of the prehallux. This reduction, however, may be regarded as advantageous, for the fewer the number of joints in an organ employed for digging, the greater will be its efficiency. Thus we find in *C. systoma* a single large piece constituting the prehallux\*.

It may be required why I homologise the single element of the prehallux of *Cacopus* with the distal piece and not with the proximal one in that of *Rana*. As the latter piece is in contact with the os naviculare, just as that of the prehallux of *Cacopus* is, one may be inclined to the alternative opinion mentioned. But a careful reference to the text-fig. 12 A, B, and C will show that my view is the more probable one; for it will be seen that while in *Rana tigrina* the distal piece numbered 4 undoubtedly corresponds to the same piece 4 either in *Rana breviceps* or in *Cacopus systoma*, in the latter two species the proximal piece 1 of the former has disappeared. According to the alternative view, one will have to say that the distal piece 4 of *Rana tigrina*

\* I venture to suggest that the so-called spade of the "Spade-footed Toad" or *Pelobates* of Europe is also the prehallux modified.

has disappeared in *Rana breviceps* and *Cacopus*, and the proximal piece 1 has acquired a shape similar to piece 4; this explanation appears more ingenious than natural. Further, in accordance

Text-figure 12 (A, B, and C).



- A. The bones of a pes of *Rana hexadactyla*. Lettering same as in A of text-fig. 11. It will be noticed that the prehallux consists of four pieces.
- B. The same of *Rana tigrina*. The prehallux is made up of only two pieces, viz. 4 and 1; 2 and 3 have probably disappeared. One may alternatively assume that 3 and 4 of *R. hexadactyla* have been omitted, and that 4 in *R. tigrina* corresponds to 2 in the latter. Lettering same as in text-fig. 11 A.
- C. The same of *Rana breviceps*. The prehallux is composed of but a single piece, like that of *Cacopus*. Lettering same as in text-fig. 11 A.

with the function of the prehallux in these frogs, it will be a distal piece which will come into direct play, and it will consequently lend itself to an adaptation in shape and size.

In this toad a further specialisation of the digit in question seems to have been brought about in its relation to the tarsus. It is firmly attached to the os naviculare, as has been already described in connection with the latter, and through the intervention of the same it articulates exclusively with the astragalus. This articulation, I should think, in combination with the action of the muscles attached to it and to the tarsal bone mentioned, bestows a considerable advantage in the act of burrowing (text-fig. 11 **B** and **C**). In *R. tigrina* and *R. breviceps* the specialisation has not been carried to that extent; the same indirect articulation of the prehallux with the astragalus is only partial, as the first digit still continues to articulate with the latter indirectly through the os naviculare; further, the prehallux and the tarsal bone connected with it are, in these frogs, much less calcified, and consequently they are less rigid and hard. Again, the *plantaris* muscle, which has no relation with the prehallux in *Rana*, has a connection with the same in this toad, in that it is indirectly inserted on to the latter by means of a fascia (text-fig. 11 **C**).

It is exceedingly interesting to find the digit, which is generally believed to be a vanishing structure in the Anura, re-asserting itself under suitable conditions and becoming an organ of no mean importance to its possessor. This specialisation of the prehallux among the species of two different families, viz. the Engystomatidæ and the Ranidæ, may be regarded as a case of convergence.

The "outer metatarsal tubercle" of this toad, though smaller than the inner one, consists likewise of a single cartilaginous piece covered with a horny dermal layer. I identify this as the "os sesamoide" (Ecker, p. 106) of *Rana*, which is a cartilaginous element situated on the plantar side of the joint between the calcaneum and the fourth metatarsal bone. In this latter position exactly I found the cartilage of the "outer metatarsal tubercle" situated in *C. systoma*, so that this also is no new structure developed by this toad, but is only a specialised and an exaggerated one of what is normally present in *Rana*. Nevertheless, it would seem that a remarkable specialisation had been brought about in its alliance with no less an important muscle than the *gastrocnemius*. To this "os sesamoide" is exclusively inserted the narrow, attenuated yet strong band of the *aponeurosis plantaris*. This implies that an important calf muscle is concerned in the working of the "outer metatarsal tubercle" (text-fig. 11 **C**).

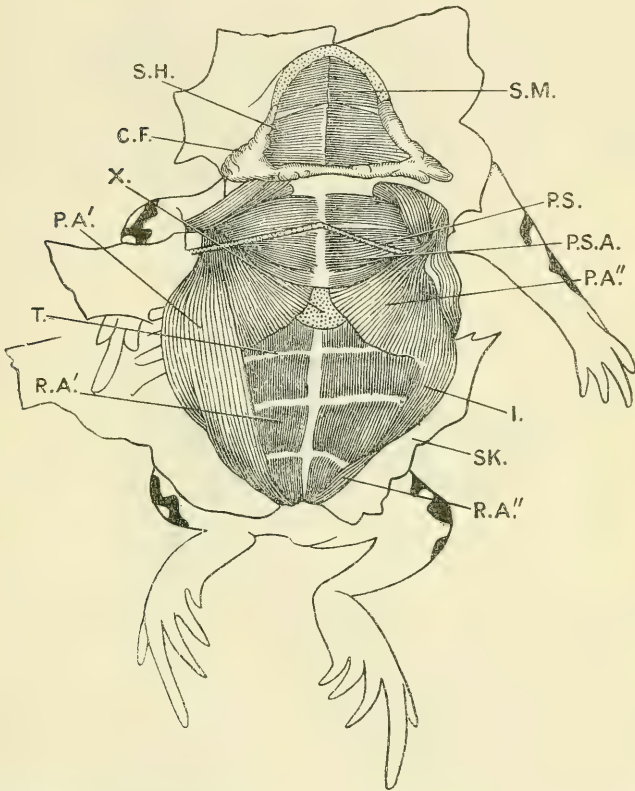
#### 7. The Musculature.

The muscles of the hyoid apparatus and of the floor of the mouth are characterised by a great specialisation in this toad, a remarkable fact observed also by Beddard (1) in three other members of the same family. However, in the details of the specialisation, excepting perhaps in the *sternohyoideus*, one does

not find any features which could be distinguished as common to *Cacopus* and to those described by the authority mentioned.

We will follow Beddard in calling the posterior portion of the *sub-maxillaris* the *sub-hyoideus*, and in restricting the original name to the anterior portion of the same muscle. Now this "*sub-hyoideus*" is much larger than the *sub-maxillaris*—the

Text-figure 13.



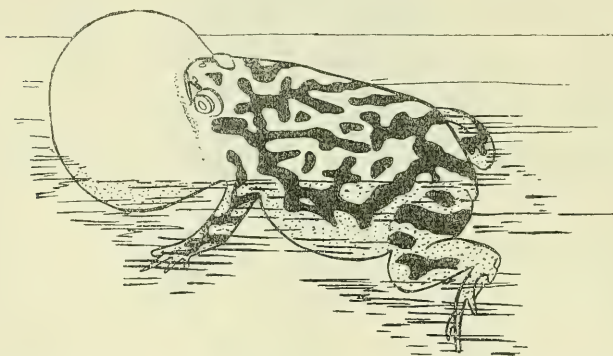
Certain muscles on the ventral surface of the trunk and head of *Cacopus systema* have been exposed. T., an *inscriptio-tendina* of the inner division of the *rectus-abdominis*; C.F., ventral extension of the "cervical fat-body"; I., the spot where the outer division of the *rectus-abdominis* and that of the *portio-abdominis* are attached to the skin; P.S., pectoral septum; S.M., *sub-maxillaris*; S.H., *sub-hyoideus*. For other letters see key-list of abbreviations.

reverse of what obtains in *Rana* (text fig. 13). The proportion which the former muscle assumes in the male is in conformity with the differentiation of a median vocal sac. It is a posterior portion of this muscle which, along with the skin in this region, becomes enormously expanded to form a large spherical resonator

during the time of croaking (text-fig. 14). When at rest, this part of the muscle is withdrawn and stowed away in a conspicuous double fold above the anterior portion of the same muscle.

On removing the *sub-maxillaris* and the *sub-hyoideus* several inner muscles of the floor of the mouth come into view (text-fig. 15). It is seen that the transverse fibres of the *sub-mentalis* (S.M.) pass from the inner border of one mentomeckelian to that of the other, thus having apparently\* no connection with the dentary. It is also seen that a greater part of the same muscle is connected with the cartilaginous piece borne by each mentomeckelian, which has been already described in the section on the axial skeleton. Of greater interest is the *genio-hyoideus* muscle, whose origin and insertion are very different from what obtains in *Rana*. The outer portion of this muscle

Text-figure 14.



A male *Cacopus* with the vocal sac in action; drawn from life; half natural size.

The enormous distension of the vocal sac is remarkable; under natural surroundings it looked more like a float than a resonator.

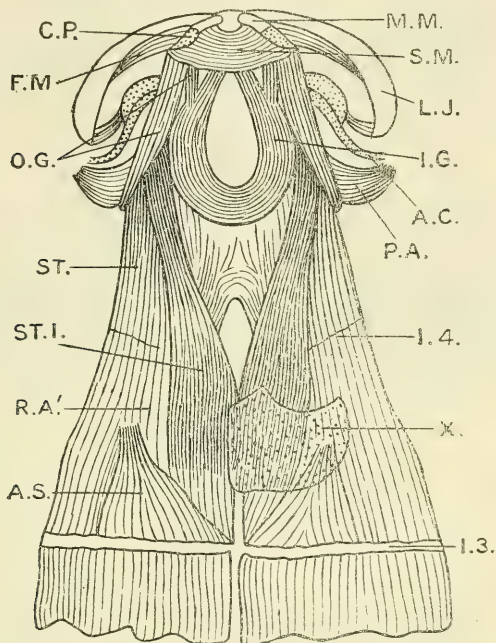
arises from the angulosplenic and passes on the outer side of the mentomeckelian cartilaginous piece and that of the *sterno-hyoideus* muscles to be inserted on to the posterior cornu (text-figs. 15 & 16 A). Though it is widely separated from the inner division, it is connected with the latter by some of its fibres, which diverge from its body at about the place of origin and become confluent with the same inner portion, so that on the right side of the toad this outer portion and that part of the corresponding inner division lying in the pre-hyoid part of the floor of the mouth have together the shape of the letter N. It will be noticed that a few of the connecting fibres are intercepted

\* It looks as though the cartilaginous part of the mentomeckelian has insinuated itself across the fibres of this muscle; for one finds between the outer side of this same part of the lower jaw several muscular fibres which I presume belong to the *sub-mentalis* (text-fig. 15, F.M.).



by the cartilaginous portion of the mentomeckelian (text-fig. 16 A). The inner divisions of the two *geniohyoideus* muscles are still further remarkable, for, in the region of the basi-hyal, they fuse\* to form an extensive median sheet of muscle with two posterior offshoots, each of which, spreading on a posterior cornu, entirely conceals the *hyoglossus* muscle in the usual position of the toad

Text-figure 15.



A view of certain superficial muscles of the hyoid and deep-lying ones of the floor of the mouth. The lower jaw (L.J.) has been divaricated; the *sub-maxillaris* and the "*sub-hyoideus*" have been removed; a right half of the xiphisternum has been cut away in order to expose at their origins the inner portion of the *sternohyoideus* (ST. I.) and the "*abdominis-sternalis*" (A.S.). R.A., continuation of the "inner division of the *rectus-abdominis*" as the "outer portion of the *sternohyoideus*" ST.; I.3 and I.4, third and fourth *inscriptio-tendina* of R.A.' respectively; F.M., certain muscle-fibres between the lower jaw and the cartilaginous part of a mentomeckelian. For other letters consult the key-list of abbreviations.

during dissection. The insertion of the former, in consequence of its extensiveness, is extraordinary; for it consists of a perimeter of the inner lateral edges of the two posterior cornua and the hind border of the basi-hyal enclosed between these two cornua, thus forming a parabolic curve (text-fig. 16 B, G.').

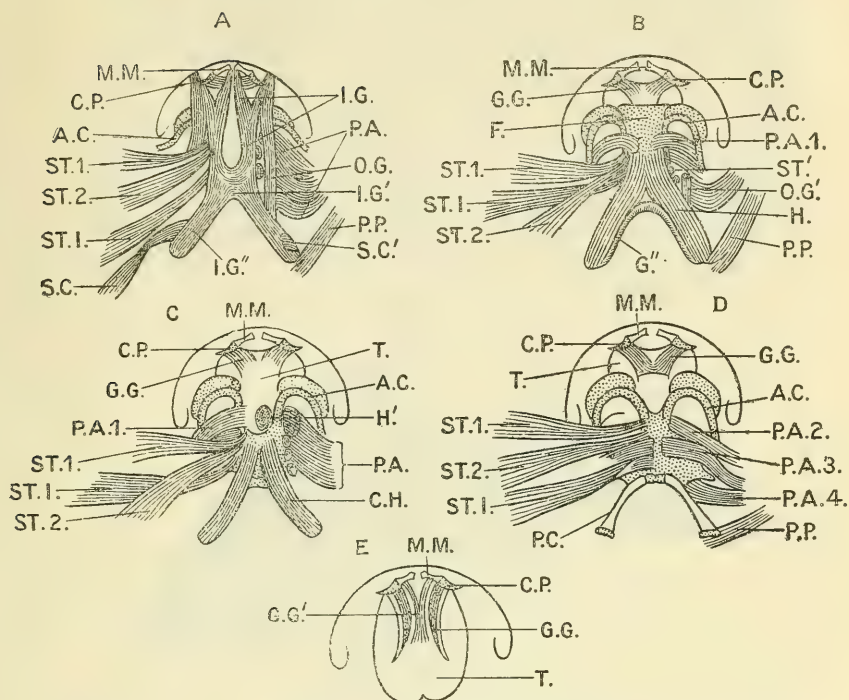
The single "*outer portion of the sternohyoideus*" (or the

\* A condition similar to this has been observed by Beddard (1) in *Breviceps*.

sternohyoideus proper) has differentiated into two separate muscles in this toad, one lying above the other. This differentiation starts at the fourth and the last *inscriptio-tendina* of the *rectus-abdominis*. A similar division of this muscle has been observed in *Breviceps* and *Hemisus* by Beddard (1). What corresponds to the "inner (median?) portion of the same muscle" is a strip which arises entirely from the xiphisternal plate (text-figs. 15, ST. I., & 16). Now, these three divisions of the *sternohyoideus* are separately inserted on to the body of the hyoid, one behind the other and in close succession; none of the fibres, however, is attached either to the posterior cartilaginous process of the same hyoid plate or to the posterior cornu.

On removing the hyoid portion of the inner *genioglossus* muscles, the *hyoglossus* pair comes into view which, in turn, conceals another muscle in the ordinary position of dissection. The thick, coarse fibres in the interior of the azygous portion of the *hyoglossus* are either sinuous or twisted like a corkscrew. As this muscle is the retractor of the tongue, this condition, at rest, of the fibres mentioned suggests that they are capable of being stretched to a greater extent than usual so as to permit the tongue to reach a comparatively longer distance. In *Rana* the paired portion of the same *hyoglossus* is the innermost muscle in contact with the lower surface of the posterior cornua; but, in this toad, there intervenes a new pair of muscles between the two, which arises from the distal quarter of the latter, and is inserted to a strong fascia spreading in the space enclosed by the proximal parts of the anterior cornua and the anterior margin of the basi-hyal (text-fig. 16 C, C.H.). Among the muscles connected with the hyoid skeleton, there are several which are solely attached to the posterior cornua on the one side and to the bones of the skull and of the pectoral girdle on the other. Now, it is likely that this new muscle, which we may term the *cornuoideus-posterior*, counteracts a probably too powerful pull of these muscles in question on the same cornua by binding the latter with the basi-hyal plate. One finds another new pair of muscles, not recorded in *Rana*, arising from the xiphisternum and running forward beneath the auricle to be attached to the posterior cornu (text-fig. 16 A, S.C.); this may be called the *sterno-cornuoideus* in accordance with its origin and insertion. The petrohyoideus muscles are distinguished by their robust development and by their numerous insertions. The *petrohyoideus-anterior* arises from the pro-otic by means of a single tendon, and spreads over the outer surface of the pharynx, to whose wall all its fibres are more or less adherent (text-fig. 16 A, B, C, and D). According to the several insertions of this muscle, one may recognise the following divisions: (1) a band, P.A. 1, inserted on to the fascia in relation with the proximal parts of the anterior cornua; (2) another anterior portion, P.A. 2, attached to the root of the same cornua; (3) a small narrow division, P.A. 3, attached to the lower surface of the basi-hyal; and (4) a

Text-figure 16 (A, B, C, D, and E).

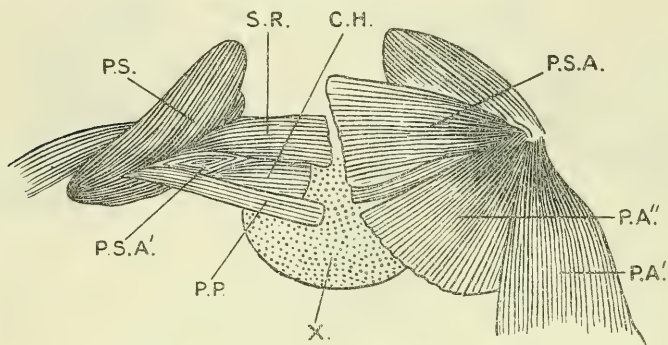


- A. The deep muscles of the hyoid and of the floor of the mouth. The *sub-mental* has been taken away. The *sterno-hyoid* muscles on the right side have been severed at their origins and deflected while those on the left have been removed. O.G., an outer division of the *geniohyoid*; I.G., an inner one of the same; I.G', a fused median portion of I.G.; I.G'', a posterior offshoot of I.G.' concealing a *hyoglossus* below; S.C., *sterno-cornuoides*; S.C', cut end of the same. For other letters consult the key-list of abbreviations.
- B. The deep muscles of the hyoid continued; the *geniohyoid* muscles have been removed excepting those fibres of I.G.' and I.G.'' at their insertion (G'') which, as will be seen, is a parabolic curve. ST.1 and ST.2, the two divisions of the "outer portion of the *sternohyoid*" or the "*sternohyoid* proper." P.A.1, an anterior division of the *petrohyoid*; O.G', cut end of the outer *geniohyoid*; ST', cut ends of the *sternohyoid* muscles; F., fascia; H., *hyoglossus*. Other letters as in A.
- C. The same muscles continued. The *hyoglossus* in the region of the basihyal has been cut away. C.H., "*cornuoides-posterior*"; H', cut end of the azygous *hyoglossus*; P.A., *petrohyoides-anterior*; P.A.1, an anterior division of the latter. The remaining letters as in the other figures of this text-figure.
- D. The same muscles continued. The "*cornuoides-posterior*" has been removed. P.A.2, P.A.3, and P.A.4, the several bundles into which the *petrohyoides-anterior* separates itself before its insertion; P.P., *petrohyoides-posterior*. For other letters consult the key-list of abbreviations.
- E. Certain muscles of the tongue viewed from below. The median and azygous part of the *genioglossus* (G.G.) has been cut in the middle in order to expose the muscle G.G', which corresponds to the outer portion of the *genioglossus*.

posterior thick division, P.A. 4, inserted on to the upper surface of the same plate. As regards the *petrohyoideus-posterior* (P.P.), while a small part of it clings to the cartilaginous free end of a posterior cornu, the bulk of the fibres pass above the latter and are inserted to the pharynx, a few fibres reaching also to the larynx. I could not find any trace of the *omo-hyoid* muscle, a negative feature observed also in *Breviceps* and *Hemisis*.

Of the muscles of the tongue, it may be noted that the relative position of the two divisions of the *genioglossus* has undergone an alteration. The one corresponding to the outer part in *Rana* lies above the other corresponding to the median part of this muscle. Further, the former has shifted its insertion from the mucous membrane of the floor of the mouth to the body of the tongue (text-fig. 16 E).

Text-figure 17.



View of certain muscles of the chest. On the right side the *portio-sternalis-anterior* and the *portio-abdominis* have been removed. S.R., *sterno-radialis*; P.S., *portio-scapularis* or the vestigial *deltoideus*; P.S.A., *portio-sternalis-anterior*; P.S.A', cut end of the same on the right; C.H., *coraco-humeralis*; P.A', outer division of the *portio-abdominis*; P.A'', an inner division of the same muscle; X., xiphisternum.

It seems to me that the specialisation described above of the muscles of the hyoid and of the floor of the mouth is in some way connected with a more efficient method of obtaining food.

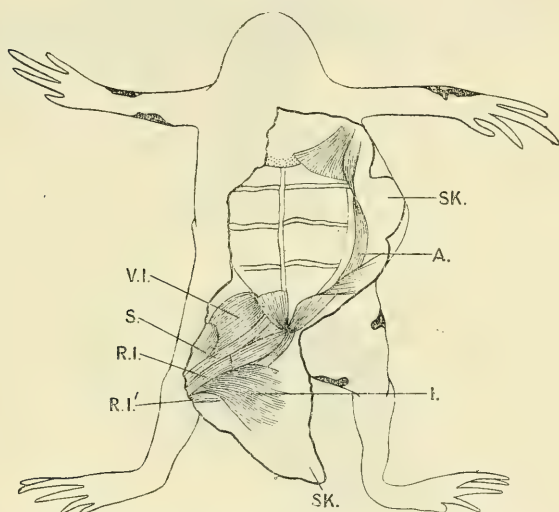
The muscles of the chest as a whole, with the exception of the *portio-sternalis-anterior* and the *portio-abdominis*, exhibit a feeble development (text-figs. 13 & 17). This, in my opinion, is mainly due to the disappearance of the pre-coracoid, the omosternum, and the episternum. For instance, the *sterno-radialis*, which arises in *Rana* from the three elements of the pectoral girdle mentioned, has its origin shifted to the inner ventral border of the coracoid, which is less extensive; consequently this muscle is vestigial\*. Again, the *deltoideus* exhibits a degeneration in the absence of one of its two divisions,

\* In this connection it may be mentioned that this muscle is absent in *Breviceps* (1).



viz. the *pars-clavicularis*. It would also appear that as the functions of these two muscles of the chest have become reduced to a minimum in this toad, a large size and an extensive origin for the same have been rendered unnecessary. According to Ecker (4), in *Rana* the *sterno-radialis* is a powerful flexor of the fore-arm, and the *deltoideus* draws the same limb forwards. These movements, though essential to a good swimmer, are in all probability of only a limited use to a terrestrial frog. Thus it becomes difficult to say whether the vestigial condition of the chest-muscles led to the disappearance of certain of the elements of the pectoral girdle, or the latter condition necessitated the

Text-figure 18.



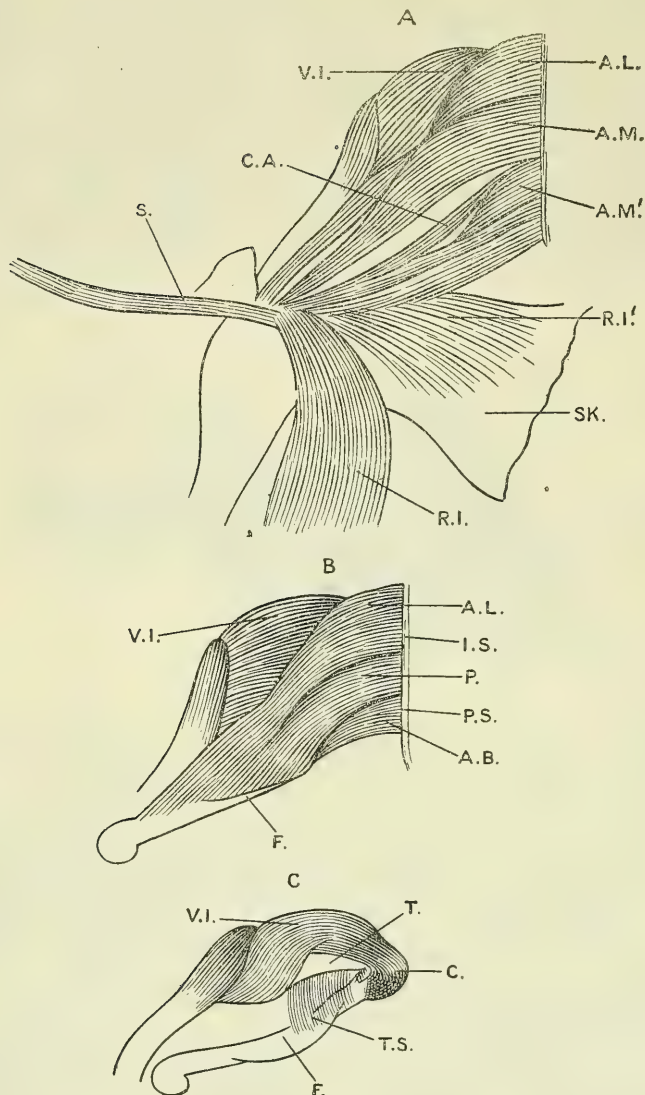
A ventral view of the trunk and a thigh with the skin cut open in order to show the relation of certain muscles with the skin. I., several fibres of the *rectus-internus-minor* (R.I.') arising from the skin (SK.) on the lower surface of a thigh; A., the region of the skin from which the outer division of the *portio-abdominis* starts and to which that of the *rectus-abdominis* is inserted; S., sartorius; R.I., *rectus-internus-major*; V.I., *vastus-internus*.

former. It is more probable that the two degenerative processes might have proceeded concomitantly.

On the contrary, one finds that the *portio-sternalis-anterior* and the *portio-abdominis* muscles have attained a great development, and the outer division of the latter has become partially converted into a cutaneous muscle (text-fig. 18). The attachment to the skin has, I should think, given additional purchase to this muscle in pulling the front limb backwards and towards the body, as happens while burrowing. These two chest-muscles are probably put to a greater use in this toad at the expense of the *sterno-radialis* and the *deltoideus*.



## Text-figure 19 (A, B, and C).



- A. Certain muscles on the lower surface of a thigh. C.A., *caput-anticum* of the *semi-tendinosus*; A.L., *adductor-longus*; A.M., *adductor-magnus*; A.M', a hind portion of the same. Other letters as in text-fig. 18.
- B. Most of the muscles on the lower part of the thigh have been removed in order to show a few deep ones. A.L., *adductor-longus*; P., *pectineus*; A.B., *adductor-brevis*; F., a crest of the femur; I.S., iliac symphysis; P.S., pubic symphysis.
- C. A view of the *vastus-internus* (V.I.) showing the details of its origin. C., capsule of the hip joint; F., a crest of the femur; T.S., a band of tendinous strips starting from a strong tendon (T).

The *rectus-abdominis* muscle of the trunk is remarkable for having shifted its origin backward from the pubes to the ischia; its outer portion is, along the greater part of its length, adherent to the skin below. This is significant when viewed along with the absence of the *cutaneus-pectoris* in this toad. At the third inscriptio-tendina of each *rectus-abdominis* one finds a small triangular portion, separated off from its main body, passing forward and attached to the upper side of the xiphisternal plate (text-fig. 15, A.S.). This muscle, which we may call "the *abdominis sternalis*," should be regarded as a differentiated part of the inner portion of the *rectus-abdominis*, for in *Rana* some of the fibres of the latter in the same situation are attached to the xiphisternum. While the *rectus-abdominis* muscles are generally thin and attenuated, the *obliquus* muscles are better developed and are thrown into transverse puckers, and bulge out prominently on the sides on account of the pressure of the enormously developed viscera.

Among the muscles of the thigh, the *rectus-femoris-anticus* is absent, the *triceps-femoris*, composed of three divisions in *Rana*, is made up of only two, and the origin of the *vastus-internus* is somewhat different. Though most of the anterior fibres of the last arise from the capsule of the hip-joint, the rest of them arise from a long tendon given off by the same capsule (text-fig. 19 C, T.). Further, this tendon is adpressed to the shaft of the femur by tendinous slips which spring from it laterally. On one side of the tendon, namely the inner lower side, these slips are so closely set as to form a band (T.S.). As regards the *rectus-internus-minor*, one finds that, on its lower side, a considerable number of fibres take origin on the skin of the thigh (text-figs. 18 & 19 A). This partially cutaneous origin of the muscle recalls a similar condition in the frogs described by Beddard (1). The *semi-tendinosus* is inserted by a narrow tendon which spreads in a triangular form over the anterior head of the tibio-fibula, in this respect differing from that of *Rana*, where the tendon in question unites with that of the *sartorius* to form an aponeurotic arch. The *adductor-longus*, the *pectineus*, and the *adductor-brevis* may be considered as forming a single muscle, for they are not distinctly delimited from one another. The greater portion of this huge muscle is hidden from view by the *sartorius* and the *adductor-magnus*, and where it is inserted on to the shaft of the femur its fibres along the middle are firmly attached to a crest of the femur already mentioned (text-fig. 19 B).

### 8. Summary.

(1) In the pharynx a new structure is situated to which the status of an organ may be given, and it has been accordingly named "the pharyngeal organ of *Cacopus systema*."

(2) Sub-cutaneous as well as sub-peritoneal fat-bodies are normally present in this toad; while the former are developed

in relation to the lymphatic septa, the latter are probably deposited in connection with the peritoneal membrane. Their function, as has been ascertained, is to assist in the general metabolism of the body during aestivation.

(3) The stoutness of this toad is, in the first instance, due to the enormously developed viscera. This condition is improved upon by the inclusion of a part of the thigh into the contour of the trunk and by the enlarged sub-cutaneous lymph-sinuses.

(4) In the skeleton the vestigial state of several of the bones of the head is remarkable. This and the consequent engystomatous mouth are, in my opinion, related in some unknown manner to the nature of the diet, which consists almost entirely of termites\*, winged or wingless according to the season. Witness, in this connection, the similar effect produced by a similar diet on the Myrmecophagidæ among Mammals.

(5) It is noteworthy that the pre-hallux of *Rana*, usually regarded as a degenerate digit, has in this toad become an organ with a definite function, viz. the so-called "inner metatarsal tubercle."

(6) While certain muscles, for example the *sterno-radialis* and the *deltoideus*, show a remarkable degeneration, other muscles, for instance the muscles of the hyoid and of the floor of the mouth, exhibit an equally remarkable specialisation. The muscles examined also show important differences in their relative dimensions, origins, and insertions. Certain new muscles are present which have been already described, while three muscles are absent, viz. the *cutaneus-pectoris*, *omo-hyoid*, and the *rectus-femoris-anticus*. Again, certain non-cutaneous muscles of *Rana* have acquired a partial connection with the skin, for example, the *rectus-internus* and the *portio-abdominis*. Assuming the muscular anatomy of *Rana* to be typical of the Anura, one may trace the differences in the musculature of this toad to two factors, viz. the fossorial habit and the nature of its food. This creature passes the greater part of its life underground, seeking water only for breeding purposes. This implies that, while the same muscles called into frequent activity in an aquatic frog may suffer by the want of regular use, other muscles of a direct utility in burrowing are likely to be improved and exaggerated. At the same time, the curiously specialised muscles of the hyoid and of the floor of the mouth probably indicate a more efficient method of capturing insects.

(7) Beddard (1) mentions three characters which may be common to the Engystomatidæ: these are (1) the partially cutaneous origin of the *rectus-internus-minor*, the specialisation of the muscles of the floor of the mouth, and the division of the "outer portion of the *sternohyoideus*." One may say that in

\* Although it is true that insects form the chief food of frogs in general, yet a liberal diet of termites alone appears to produce the peculiar effect on the constitution which we have indicated.

these respects *Cacopus systoma* also agrees with the three genera described by him. Nevertheless, in the details of the second feature mentioned there is hardly any striking resemblance. I should add that the *omo-hyoid* muscle is generally absent among the same family, as it has not been found either in this toad or in *Breviceps* and *Hemisus*.

9. *Key-list of certain of the Abbreviations mostly unexplained in the explanations to Text-Figures.*

A.C.—Anterior cornu.	P.A.— <i>Petrohyoideus-anterior</i> .
A.H.—Articular head for the lower jaw.	P.A.'—Inner division of a <i>portio-abdominis</i> .
C.P.—A cartilaginous part of the mentomeckelian.	P.A."—Outer division of the same.
C.S.—Cartilaginous epiphysis of the sacrum.	P.M.—Premaxilla.
C.S.'— <i>Coccygeo-sacralis</i> .	P.P.— <i>Petrohyoideus-posterior</i> .
C.I.— <i>Coccygeo-iliacus</i> .	Pro.O.—Pro-otic.
Ex.O.—Ex-occipital.	P.S.—Parasphenoid.
Fr.P.—Fronto-parietal.	Q.—Quadrato-jugal.
I.G.—Inner division of a <i>genio-hyoideus</i> .	R.A.'—Inner division of a <i>rectus-abdominis</i> .
I.L.— <i>Ilio-lumbaris</i> .	R.A."—Outer division of the same.
L.D.— <i>Longissimus-dorsi</i> .	SQ.—Squamosal.
M.—Maxilla.	ST.—“Outer portion of the <i>sterno-hyoideus</i> ” or the <i>sterno-hyoideus</i> proper.
M.M.—Mentomeckelian.	ST. 1 and ST. 2.—Two divisions of the same.
Na.—Nasal.	ST. I.—An inner portion of the <i>sterno-hyoideus</i> .
O.C.—Occipital condyle.	S.H.—“Sub-hyoideus.”
O.C.H.—“Os capitato-hamatum.”	S.M.—Sub-maxillaris.
O.E.— <i>Obliquus-externus</i> .	S.M.'—Sub-mentalis.
O.G.—Outer division of a <i>genio-hyoideus</i> .	T.—Tongue.
O.I.— <i>Obliquus-internus</i> .	T.'—Terminal epiphysis of the urostyle.
O.L.—“Os lunatum.”	V.—Vomer.
O.N.—“Os naviculare” of a manus.	X.—Xiphisternal plate.
O.P.—“Os pyramidale.”	
O.T.—“Os trapezium.”	
O.Ts.—“Os trapezoides.”	
Pr.—Pterygoid.	

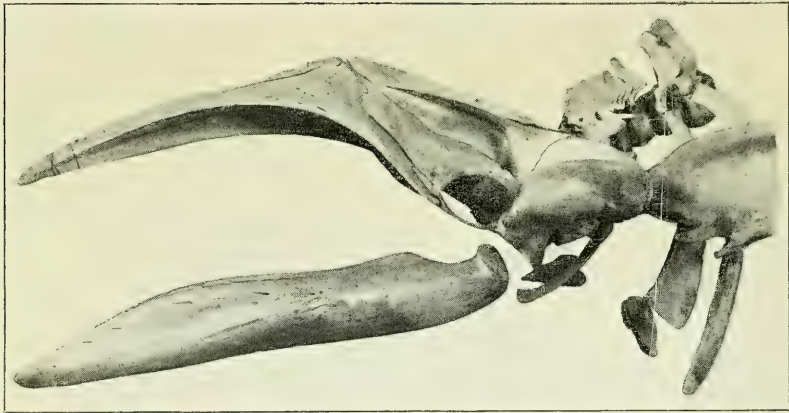
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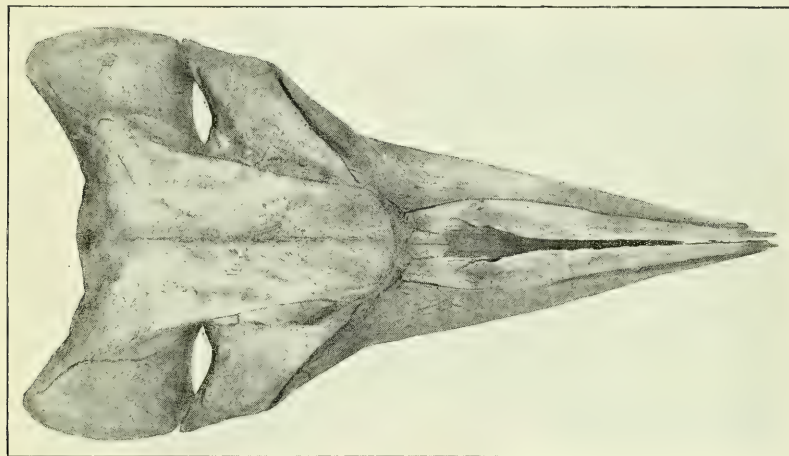
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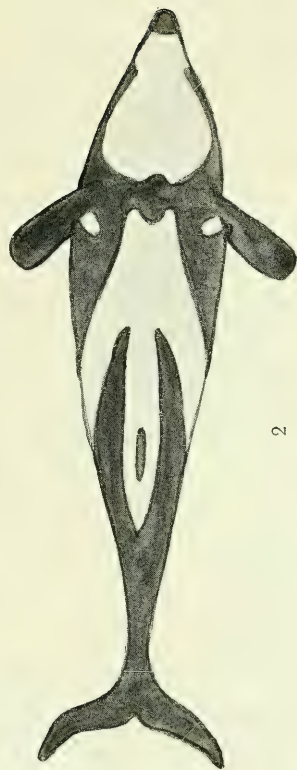


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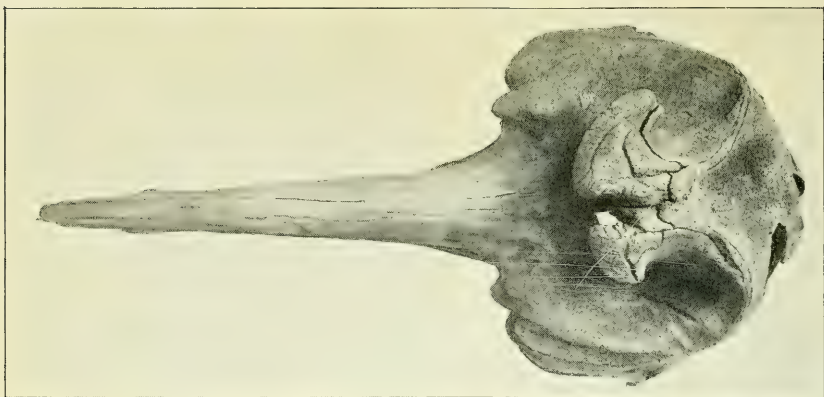
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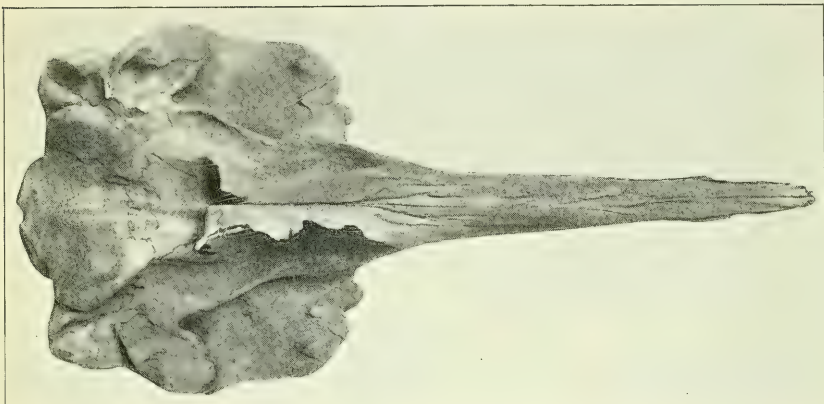




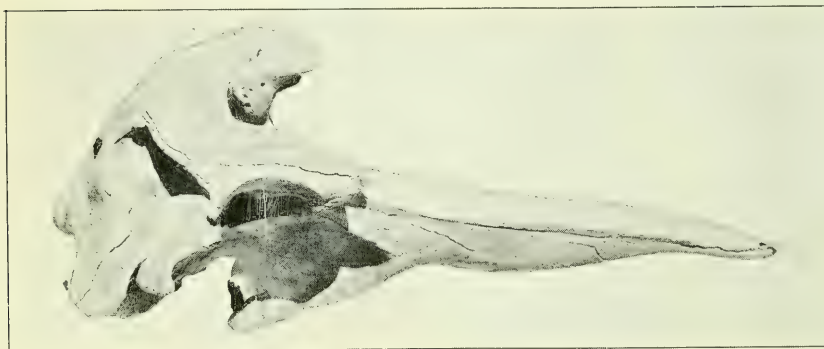




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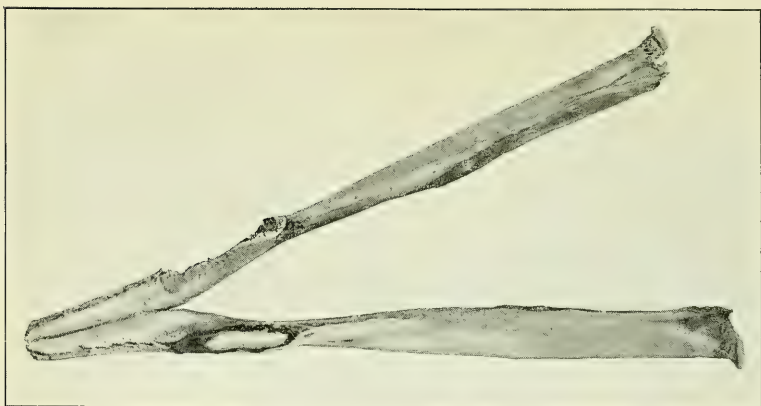


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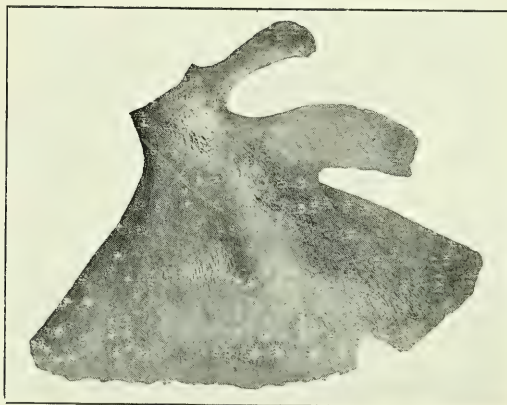




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28. A Review of the Cetacea of the New Zealand Seas.—J.  
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Wellington, N.Z.

[Received May 18, 1922: Read June 13, 1922.]

(Plates I.—IV.)\*

Except the popular accounts by Waite, and by Hutton and Drummond, no general list of the New Zealand Cetacea has been published since Hector's paper on the Delphinidæ in 1887. Having a number of notes made on various occasions to put on record, I take the opportunity of reviewing the Whales and Dolphins of our seas. The recorded knowledge of the group is very incomplete; and, moreover, some errors are apparent. The museums at Wellington and Christchurch contain a fair number of skeletons; those of Dunedin and Wanganui fewer. The only representatives of the Cetacea in the Auckland Museum appear to be three skulls. The specimens in Christchurch and Dunedin have, in the main, been recorded, but in Wellington and Wanganui there are some skeletons of considerable interest which have not hitherto been described. These are mentioned in the present paper. Besides cataloguing the specimens in the principal museums in New Zealand, I have included those specimens from New Zealand that I have been able to trace in the museums of Australia, America, and Europe. Many of these I have examined. The short descriptions given with the lists refer mainly to variable characters; and, where I myself have not examined the specimen, the author from whom I have quoted is given. An attempt has also been made to give the generic and specific names in accordance with the International Rules of Zoological Nomenclature. The literature on the Cetacea is very extensive, but some of it has to be used with caution. This applies to many of the writings of Dr. J. E. Gray, who unfortunately gave new names on quite insufficient grounds, sometimes founding genera and species on drawings and photographs he appeared not to understand. I have quoted only the principal references, including those where new names are proposed or where there are descriptions based on specimens.

I cannot claim to have added a single species to the list of New Zealand cetaceans; on the contrary, I have omitted two, *Delphinapterus leucas* and *Hyperoodon planifrons*, and hope that the evidence that neither belongs to our fauna will be accepted.

It will appear from the following account that there is much to be learned about the distribution and habits of the cetaceans of our seas; moreover, collection of perfect skeletons and descriptions of the external characters of the animals is much to be desired. In some cases the species are only known from skulls or skeletons.

\* For explanation of the Plates, see p. 585.

It is hoped, therefore, that the present paper will be found useful in bringing together what is known on the subject, so that the gaps in our knowledge may be filled up. A great deal of information could be gained if, when a whale or dolphin is stranded, a description and, if possible, a photograph were sent to the nearest museum. By this means the animal might be correctly identified, and if belonging to a rare species, steps might be taken to preserve the skeleton.

For supplying lists of specimens in the institutions under their charge, I have to thank the Director, British Museum (Natural History), London, the Secretary, United States National Museum, Washington, D.C., and the Director, Muséum d'Histoire Naturelle, Paris.

#### BALÆNA.

*Balæna* Linné, 1758, Syst. Nat. ed. 10, p. 75; type, *B. mysticetus* L. *Eubalæna* Gray, 1864, Proc. Zool. Soc. 1864, p. 201; type, *Balæna australis* Desmoulins. *Caperea* Gray, 1864, l. c. p. 202; type, *Balæna antipodarum* Gray.

#### BALÆNA AUSTRALIS.

*Balæna australis* Desmoulins, 1822, Diet. Class. Hist. Nat. vol. ii. p. 161 (Cape of Good Hope); Waite, 1909, Subant. Is. N.Z. vol. ii. p. 549. *Balæna antipodum* Gray, 1843, in Dieffenbach's Travels in N.Z. vol. ii. p. 183 (New Zealand), pl. 1, lettered *B. antipodarum*. *Caperea antipodarum* Gray, 1866, Cat. Seals & Whales Brit. Mus. p. 101; Proc. Zool. Soc. 1873, p. 143. *Balæna antipodarum* Gray, Dieffenbach, Travels in N.Z. vol. i. p. 44; Van Beneden & Gervais, 1880, Ostéogr. Cet. p. 46, pl. 3. *Eubalæna australis* Desm., Hector, 1872, Trans. N.Z. Inst. vol. v. p. 156; id. 1878, l. c. vol. x. p. 333. *Balæna hectori* Gray, 1874, Ann. Mag. Nat. Hist. ser. 4, vol. xiii. p. 56. *Macleayius australiensis* Gray, 1873, Ann. Mag. Nat. Hist. ser. 4, vol. xi. p. 75; id. Proc. Zool. Soc. 1873, p. 130; id. 1874, Trans. N.Z. Inst. vol. vi. p. 90, pls. 16, 17.

The Southern Right Whale, which is confined to the South Temperate and Subantarctic Oceans, appears to differ from the Nordcaper (*B. glacialis*) in the number of ribs and other osteological features. It was formerly very abundant in the New Zealand seas, but has been almost exterminated by whalers. During the first half of last century immense numbers were killed, and of these usually more than half were lost (see Hocken, Proc. N.Z. Inst. vol. iii. p. 69, 1871). The females visited the bays to calve during the months of May, June, and July, and during this period both the cows and calves were killed. Later in the season the whaling-vessels cruised in the "off-shore grounds." Whaling-stations are at present established at Picton and Kaikoura, motor-launches being engaged for procuring the whales. Five Right Whales were brought into Picton in 1915-16 and one in 1917; from the Kaikoura station three were killed in 1917-18. A



whaling-station was formerly established at Campbell Island. Waite states that Right Whales are nearly always seen during the southern cruise of the Government vessels.

*Cook Strait*.—(a) Dieffenbach describes and figures (vol. ii. pl. 1) a Right Whale, stranded in Jackson's Bay, Tory Channel, in 1839. On this figure, Gray in the same work founded *Balæna antipodum*; the plate, however, was lettered *Balæna antipodarum*. The tympanic bone later referred to this species (Gray, 1866) belonged to *Neobalæna marginata*. *Caperea* was founded on *B. antipodarum*, and the tympanic bone mentioned. (b) Tory Channel. Scapula in Dominion Museum. Described by Gray as *Balæna hectori*. Acromion distinct.

*Canterbury*.—(a) Skeleton in British Museum sent by von Haast. Described by Gray (*M. australiensis*). Vertebrae 54. Cervicals and first dorsal fused into one mass by their centra. Sternum oblong,  $6\frac{1}{2} \times 5$  in. Scapula with broad compressed acromion. (Gray.) (b) Akaroa Harbour. Skeleton with baleen in the Paris Museum. Taken by Berard and Arnoux, of the French corvette, 'Le Rhin.' Described by Van Beneden and Gervais, and by Hector (1878). Vertebrae: C. 7, D. 15, L. 11, Ca. 21=54. Cervicals fused. Scapula with acromion represented only by a ridge. Phalanges: 2, 5, 6, 5, 4. Distal end of first rib expanded and two-headed. Sternum triangular, sinuated, sides convex, articular facets at front angles. (From van Beneden and Gervais's description and figure.) Van Beneden in two places states the total number of vertebrae to be 53, but figures for each portion of the vertebral column are also given as above stated.

*Otago*.—Skeleton with baleen in the Otago Museum. Described by Hector (1878). Young specimen 29 feet long. Vertebrae: C. 7, D. 14, L. 11, Ca. 22=54. Six cervicals united by their centra. Caudal region imperfect. Ribs 14. Scapula with a well-developed narrow acromion. (Hector states that the dorsals number 15, and the ribs should probably be 15.)

#### NEOBALÆNA.

*Neobalæna* Gray, 1870, Ann. Mag. Nat. Hist. ser. 4, vol. vi. p. 155; type, *Balæna marginata* Gray.

#### NEOBALÆNA MARGINATA. (Pl. I.)

*Balæna marginata* Gray, 1846, Zool. 'Erebus' & 'Terror,' p. 48, pl. 1 (West Australia). *Balæna antipodarum* Gray, 1864, Proc. Zool. Soc. p. 202 (tympanic bone). *Balæna marginata* Gray, Hector, 1870, Trans. N.Z. Inst. vol. ii. p. 26, pl. 26; id. 1870, Ann. Mag. Nat. Hist. ser. 4, vol. v. p. 221. *Neobalæna marginata* Gray, 1870, Ann. Mag. Nat. Hist. ser. 4, vol. vi. p. 156; id. 1873, l. c. vol. xi. p. 108; id. 1871, Trans. N.Z. Inst. vol. iii. p. 123; id. 1874, l. c. vol. vi. p. 93. Hector, 1873, Trans. N.Z. Inst. vol. v. p. 155; id. 1875, l. c. vol. vii. p. 271, pls. 16, 17; id. 1878, l. c. vol. x. p. 331.

The Pigmy Right Whale has occurred a number of times on the New Zealand coast. Elsewhere it has been recorded from West Australia and South Australia. *Balæna marginata* was founded on three plates of baleen now in the British Museum. A skull from Kawau was next recognized as belonging to the same species, and was described by Hector (1870, p. 26). This was constantly referred to by Hector and others (see Palmer, Index Gen. Mamm. p. 452, 1904) as the "type" of the species, but this is obviously wrong. The type of *Balæna marginata* is the baleen from West Australia in the British Museum.

*Kawau*.—Skull in Dominion Museum, Wellington. Described by Hector (1870). Hector afterwards referred to this as the type skull. On Hector's description Gray separated the species from *Balæna* under the generic name *Neobalæna*. (Pl. I. figs. 2 & 3.)

*Oharia, Cook Strait*.—Skeleton in Dominion Museum, Wellington. Vertebrae: C. 7, D. 18, L. 2, Ca. 14=41. Cervicals fused. Ribs 17, of which 2nd to 5th are two-headed.

*Canterbury Coast*.—Skeleton in Australian Museum, Sydney.

*Stewart Island*.—(a) Skeleton with baleen in British Museum. Described by Hector (1875, 1871). In this description the number of vertebrae and ribs appears to be incorrectly stated. Compare the description by Beddard ('Book of Whales,' p. 141, 1900.) (b) Skeleton in Dominion Museum, Wellington. Skull symmetrical. Viewed from above, the general form is triangular, broadest behind where at the angles the supraoccipital and squamosals meet; from here it tapers at first gradually to the edge of the orbits, then suddenly to opposite the nasals; thence follows a long, tapering, pointed rostrum with slightly concave sides. Viewed from the side, the upper contour of the skull is nearly straight from condyles to vertex, then depressed at a broad angle and slightly bowed to the tip of the rostrum. Premaxillaries narrow, of nearly uniform width, their inner edges meeting as an acute ridge in front, but flattening out near the blow-hole and twisting so that the outer edges form ridges each side of it. Maxillaries broad behind, suddenly contracting to opposite the nasals, tapering to a point anteriorly, not extending as far forward as the premaxillaries. The exposed lateral portions of the frontal form two broad quadrangular plates, overlapping the posterior portion of the maxillaries, and well below the level of the supraoccipital, slightly concave centrally, but arched over the orbits. A narrow strip only of the frontal exposed between the supraoccipital and nasals. Wide deep lateral channels between upper and lower horizontal expansions of the supraoccipital. On the palatal aspect of the skull the maxillaries form a sharp central ridge, between which the vomer is exposed. Pterygoids meeting along the middle line, flat behind but anteriorly forming a ridge continuous with that of the maxillaries. Rami of mandible massive, compressed, angled above and below; nerve foramina near the upper edge. (Pl. I. fig. 1.) Vertebrae: C. 7, D. 18, L. 1, Ca. 14=40. Cervicals fused into a single mass

by their centra and neural arches. Spinous processes forming a high acute vertical ridge; posteriorly the sides of the neural arches project as laminated plates. Seven nerve foramina on each side. Anteriorly there is a large vertical lateral process with three projecting knobs in a vertical line and a fourth behind the upper one. The first dorsal has a forwardly-directed spinous process, short-pointed transverse processes, and bears no ribs. Transverse processes in the second dorsal angular, in the third and fourth wider and twisted, in the remainder very broad and flat, with the anterior sides projecting considerably in advance of the centra. Articular facets on the distal ends of the transverse processes of the 2nd to 10th dorsals. Spinous processes broad and flat, with lamellar metapophyses from the third dorsal backwards. Lumbar vertebræ similar to last dorsal; the transverse processes longer in an antero-posterior than in a transverse direction. The first seven caudals bear chevrons. Transverse processes reduced to ridges on the fifth, last neural canal evident on the 8th caudal, which is the last of the compressed form. In all the vertebræ behind the cervicals, the epiphyses are marked by distinct sutures. Ribs 17, articulated to the 2nd to 18th dorsals. First single-headed, broad and truncate distally, 2nd to 5th double-headed, but the capitula not reaching the centra. Remainder single-headed, with very broad, flat blades, except the last two pairs, which are small and narrow. The last twelve ribs are set at nearly a right angle to the transverse processes of the vertebræ. Scapula much wider than long, flat with a very slight spine; acromion directed forwards, flat, moderately broad, and tapering; coracoid short and narrow. Sternum shield-shaped, notched in front, one articular facet on each side for the first rib.

*Locality not known.*—(a) Skull of young in Auckland Museum. Described by Hector (1875). (b) There is a skeleton or portion of one in the Paris Museum sent by Mr. Trail in 1879. It probably came from Stewart Island.

#### BALÆNOPTERA.

*Balænoptera* Lacépède, 1804, Hist. Nat. Cét. pp. xxxvi. 114; type, *B. acuto-rostrata* Lacép.

To the four recent species constituting this genus, 18 generic names have been applied. Of these, eight were founded by Dr. J. E. Gray, whose prolific writings on the Cetacea resulted in more synonyms than valid names, and are the despair of later students.

#### BALÆNOPTERA MUSCULUS.

*Balaena musculus* Linné, 1758, Syst. Nat. ed. 10, p. 76 (Scotland) (not *Balænoptera musculus* auct.). *Balænoptera sibbaldii* Gray, 1847, Proc. Zool. Soc. 1847, p. 92; Waite, 1912, Rec. Cant. Mus. vol. i. p. 333, pls. 69–71; id. 1912, Guide Whales & Dolph. N.Z. p. 10, pls. 1–3. *Balænoptera musculus* Linné, Waite, 1909, Subant. Is. N.Z. vol. ii. p. 550.

The Blue Whale, which has a very wide range and is exceedingly abundant in the Antarctic Ocean, has only once been recorded with certainty on the New Zealand coast.

*Okarito*.—Skeleton in the Canterbury Museum. The dead whale came ashore near Okarito in February 1908. Described by Waite. Vertebæ: C. 7, D. 15, L. 14, Ca. 28=64. Cervicals free. Ribs 15, 2nd to 5th two-headed. Transverse processes of first lumbar vertebrae with articular surfaces. Sternum 56 cm. long, with five processes; one posterior, long; two lateral, triangular; two anterior diverging, truncate. Pelvic bones about 30 cm. in length, posteriorly bent downwards at nearly a right angle, each with a small detached bone about 2 cm. long above. Phalanges: 0, 7, 8, 8, 5.

*Coal Point, Otago*.—A large whale came ashore here in 1873. Some plates of baleen only were preserved, and were described by Hutton (Trans. N.Z. Inst. vol. vii. p. 266, 1875). They probably belonged to this species.

#### BALÆOPTERA PHYSALUS.

*Balæna physalus* Linné, Syst. Nat. ed. 10, p. 75 (European seas) (*Balænoptera musculus* auct.). *Physalus australis* Desm., Hector, 1875, Trans. N. Z. Inst. vol. vii. p. 257, pl. 18; id. 1878, l. c. vol. x. p. 336. *Balænoptera australis* Desm., von Haast, 1883, Proc. Zool. Soc. 1883, p. 592. *Balænoptera musculus* (not Linné) Parker, 1885, Trans. N.Z. vol. xvii. p. 3, pl. 6. *Stenobalæna xanthogaster* Gray, 1874, Ann. Mag. Nat. Hist. ser. 4, vol. xiv. p. 305; "Sulphur-bottom," Hector, 1874, Ann. Mag. Nat. Hist. ser. 4, vol. xiv. p. 304.

This is the common Finner of both northern and southern seas. It is occasionally cast ashore on the New Zealand coast.

*Nelson*.—Stranded at entrance of Waimea River, 1883. Skeleton in Otago Museum. Described by Parker. Vertebæ: C. 7, D. 15, L. 15, Ca. 25=62. Ribs 15, of which 2nd and 3rd are two-headed, last rib less than half the length of the one in front. Sternum with posterior process longer than the lateral ones. Baleen slate-colour with white fibres.

*Cook Strait*.—Stranded at Port Underwood, 10th June, 1874. Skeleton in Dominion Museum, Wellington. Described by Hector. On Hector's description Gray founded the genus and species *Stenobalæna xanthogaster*. Vertebæ: C. 7, D. 15, L. 15, Ca. 25=62. Ribs 15, of which 2nd and 3rd are two-headed. Sternum with posterior process shorter than laterals.

*New Brighton Beach*.—Stranded 1881. Skeleton described by Haast. Vertebæ: C. 7, D. 15, L. 15, Ca. 25=62. Pelvic bone 13 in. long, 6 in. broad. Sternum with the posterior process shorter than the laterals. (Von Haast.)

#### BALÆOPTERA BOREALIS.

*Balænoptera borealis* Lesson, 1828, Hist. Nat. Cet. p. 342; Lillie, 1915, 'Terra Nova' Exped., Zool. vol. i. p. 117, pl. 7.



The Sei Whale does not appear to be common south of the Equator. The following are the only known occurrences of the species in New Zealand waters:—

*Off Bay of Islands.*—(a) Exterior described by Lillie. Baleen black, with fine greyish-white bristles. (b) A male specimen, 14 m. long, was brought into the whaling-station at Whangamumu during my visit on the 5th December, 1911. It had been harpooned, the weapon passing right through the body and exploding in the water. Colour above slate, sides mottled, below silvery white; iris dark brown; baleen dark slate, upper inner angle streaked longitudinally with lighter, bristles white. Dorsal fin falcate. Flipper with lower edge nearly straight, upper rounded. Plaits between the fins 60, 7 or 8 more on each side behind the eye. Plaits begin about 25 cm. from the tip of flipper and anterior edge of fin. Contour of back nearly straight, suddenly depressed in front of flukes. Hairs on lower jaw in two rows; inside row with 12 on right side, 13 on left; outside row 1 on right, 2 on left side; total, 28 hairs. There are some punctures behind the hairs, and others in front of the body-plaits. Measurements: Total length, 14 m.; snout to anterior edge of flipper, 3.80 m.; snout to anterior edge of dorsal fin, 9.40 m.; height of fin, 40 cm.; length of upper edge of flipper, 115 cm.; its width, 38 cm.; height of body, about 180 cm. Baleen plates, 11.5 to 12.5 mm. apart; length of front plates, 8 cm., of longest 34 cm. The mouth was filled with small crustaceans. The colours noted above were taken shortly after the whale was killed, and are lighter than those usually recorded. Lillie makes a similar observation.

*Cook Strait.*—During a heavy gale at the end of January 1922, the carcass of an adult female of the Sei Whale floated through the entrance of Porirua Harbour and stranded opposite Paremata. It measured 53 feet in length. It had been dead some time, and caused a good deal of consternation among residents of the locality. The carcass was subsequently towed to sea and cast adrift.

#### BALÆOPTERA ACUTOROSTRATA.

*Balæoptera acutorostrata* Lacépède, 1804, Hist. Nat. Cét. vol. i. p. 197; Lillie, 1915, 'Terra Nova' Exped., Zool. vol. i. pls. 4, 5. *Balæoptera rostrata* Fabricius, von Haast, 1881, Trans. N.Z. Inst. vol. xiii. p. 169, pl. 3; Benham, 1901, Proc. Zool. Soc. 1901, vol. i. p. 278; id. 1902, Trans. N.Z. Inst. vol. xxxiv. p. 151. *Balæoptera huttoni* Gray, 1874, Ann. Mag. Nat. Hist. ser. 4, vol. xiii. p. 450; Hector, 1878, Trans. N.Z. Inst. vol. x. p. 337. *Physalus antarcticus* Gray, 1874, Ann. Mag. Nat. Hist. ser. 4, vol. xiii. p. 316.

The Pike Whale, like its congeners, is widely distributed. All the records certainly identified from New Zealand have been from the South Island. In addition to the following specimens, Proc. Zool. Soc.—1922, No. XXXIX.



however, a young Pike Whale was recorded as having been killed at Port Ahuriri, Hawke's Bay, in 1885. Variations occur with regard to the vertebral formulæ. Apparently the normal number is C. 7, D. 11, L. 13, Ca. 17=48.

*Summer, Canterbury.*—Stranded 7th February, 1880. Skeleton in Canterbury Museum. Described by von Haast. Vertebrae: C. 7, D. 11, L. 12, Ca. 18=48. Ribs 11. Sternum longer than broad. Pelvic bones rod-shaped, about 22 cm. long.

*Moeraki.*—1885. Skull (incomplete) in Otago Museum.

*Otago Heads.*—(a) Oct. 1873. Skeleton with baleen in British Museum. Described by Gray as the type of *Balaenoptera huttoni*. Measurements given by Gray (p. 451). Vertebrae: C. 7, D. 12, L. 13, Ca. 16=48. Ribs 11. (Gray.) (b) Young female cast ashore, August 1900. Exterior described by Benham (1902). Larynx described by Benham (1901). Animal figured by Lillie.

*Locality not stated.*—Skeleton in Dominion Museum, Wellington. Vertebrae: C. 7, D. 11, L. 13, Ca. 17=48. Cervicals: 2nd and 3rd fused by neural arch on right side; 4th and 5th separately fused by distal ends of upper lateral processes on right side; otherwise free. Atlas with short transverse processes; 2nd to 5th with both upper and lower transverse processes; 6th and 7th with upper transverse processes only. The 8th caudal bears the last spinous process and the last complete neural canal. Ribs 11. Sternum with the length about 4 mm. short of the breadth; posterior process long and of nearly even width. Scapula with long acromion widening towards the distal end; coracoid thick, less than half the length of the acromion.

#### MEGAPTERA.

*Megaptera* Gray, 1846, Zool. 'Erebus' & 'Terror,' Mamm. p. 16; type *Balaena longimana* Rudolphi (= *B. nodosa* Bonnaterre).

#### MEGAPTERA NODOSA.

*Balaena nodosa* Bonnaterre, 1789, Tabl. Encyl. Méth., Cét. p. 5 (New England, U.S.A.); Lillie, 1915, 'Terra Nova' Exped., Zool. vol. i. pp. 87–110, pls. 1–4. *Megaptera novae zealandiae* Gray, 1864, Proc. Zool. Soc. 1864, p. 207; id. 1866, Cat. Seals & Whales Brit. Mus. p. 128, fig. 20; Hector, 1873, Trans. N.Z. Inst. vol. v. p. 156; id. 1875, l. c. vol. vii. p. 255; Van Beneden & Gervais, 1880, Ostéogr. Cét. p. 135; Gray, 1874, Ann. Mag. Nat. Hist. ser. 4, vol. xiii. p. 57. *Megaptera lalandii* Fischer, von Haast, 1883, Trans. N.Z. Inst. vol. xv. p. 214; Hector, 1878, l. c. vol. x. p. 335. *Megaptera boops* (not Linné) Oliver, 1911, Trans. N.Z. Inst. vol. lxiii. p. 536.

The Humpback is the most common whale frequenting the New Zealand seas, but no skeleton of an animal caught within this area has been adequately described. A satisfactory description, however, has been given by Lillie of the external and internal

features from specimens brought into the Whangamumu whaling-station.

Humpback Whales regularly migrate, spending the southern summer south of New Zealand and the winter in subtropical seas. They appear at the Kermadec Islands in the latter part of August, but are most common in the group during October and November. They have their calves with them at this time. They appear off the Bay of Islands in the latter part of September, the main body passing southwards during October and November. By the middle of December no more are to be seen here. From this time until April they appear to be absent from New Zealand waters. They are hunted in Cook Strait from May to August, and appear off the Bay of Islands between the middle of April and the end of August, but are not seen at the Kermadec Islands until later in the year, as noted above. (Lillie; Oliver.)

*Kermadec Islands*.—Frequent the group in large numbers with their calves from middle of August to end of November.

*Chatham Islands*.—Baleen in the Canterbury Museum.

*Off Cape Brett*.—Regularly shot by harpoon-gun from small steam-vessel and brought into the Whangamumu whaling-station. The yearly catch varies between 40 and 70. The exterior and anatomy have been well described by Lillie.

*Cook Strait*.—(a) Porirua Harbour. Skull in British Museum. Described by Hector (1875). (b) Tory Channel. Two scapulas in Dominion Museum, Wellington. Described by Gray (1874). (c) Common, May to August. Motor-launches are engaged in whaling at Picton, catching 35 to 40 Humpbacks annually.

*Kaikoura*.—(a) Skull in Dominion Museum, Wellington. Described by Hector (1875). (b) A whaling-station is established here. Nine whales were brought in in each of the years 1918 and 1919.

*Akaroa Harbour*.—Female caught 6th May, 1875. Calf also killed. Described by von Haast (skeleton then in Canterbury Museum). Vertebrae: C. 7, D. 13, L. 10, Ca. 21=51. Cervicals free. Sternum scarcely longer than broad. (Haast.) There is a skeleton in the British Museum, presumably this one.

*Otago*.—Right tympanic and periotic bone in British Museum. Described by Gray as the type of *Megaptera nove zealandiae*.

#### PHYSETER.

*Physeter* Linné, 1758, Syst. Nat. ed. 10, p. 76; type, *P. macrocephalus* Linné.

#### PHYSETER MACROCEPHALUS.

*Physeter macrocephalus* Linné, 1758, Syst. Nat. ed. 10, p. 76 (European seas); Hector, 1878, Trans. N.Z. Inst. vol. x. p. 337; Waite, 1909, Subant. Is. N.Z. p. 551. *Catodon macrocephalus* (L.), Hector, 1873, Trans. N.Z. Inst. vol. v. p. 157. *Physeter catodon* (L.), Lillie, 1915, 'Terra Nova' Exped., Zool. vol. i. p. 118.

It has been the fashion recently to use the name *Physeter catodon* for this species, its only claim being priority of place on the page. On the other hand, its identity appears doubtful. Gray, Cope, and others applied it to the Arctic White Whale, whereas the identity of *P. macrocephalus* is clear, and the name has been in general use since its publication.

The Sperm Whale is found chiefly in tropical and warm temperate seas, though it occurs as far south as the south of New Zealand. It does not come close inshore like the Right Whale and Humpback, hence it is seldom cast ashore, although, strange to say, when this does happen, large schools are sometimes involved. It has been recorded off the Chatham and Campbell Islands. Lower jaws are preserved in the museums at Christchurch and Dunedin. There is also in the British Museum the lower jaw of a specimen taken between Cape Howe and New Zealand.

*Kaipara Coast.*—(a) A school of 27 Sperm Whales—males, females, and young—stranded in 1895. (b) School of 25 stranded opposite Dargaville, March 1918. Length varied from 22 to 45 ft.

*Cook Strait.*—Head cast ashore at Waikanae (Hector, 1873).

*South of New Zealand* (Lat. S. 44° 56', Long. E. 172° 53').—School of 12 seen 31st March, 1912 (Lillie).

#### KOGIA.

*Kogia* Gray, 1846, Zool. 'Erebus' & 'Terror,' Mamm. p. 22; type, *Physeter breviceps* Blainville.

KOGIA BREVICEPS. (Pl. II. fig. 3.)

*Physeter breviceps* Blainville, 1838, Ann. d'Anat. et Phys. vol. ii. p. 337 (Cape of Good Hope). *Kogia breviceps* Blainv., Hector, 1878, Trans. N.Z. Inst. vol. x. p. 337. *Cogia breviceps* Blainv., Benham, 1901, Proc. Zool. Soc. 1901, vol. i. p. 278; id. 1901, l. c. vol. ii. p. 107; id. 1902, l. c. vol. i. p. 54; id. 1902, Trans. N.Z. Inst. vol. xxxiv. p. 155. *Euphysetes pottsii* von Haast, 1874 (June), Trans. N.Z. Inst. vol. vi. p. 97, pl. 15; id. 1874 (Oct.), Proc. Zool. Soc. 1874, p. 260.

Though a rare whale, the Pigmy Sperm Whale has been taken in all seas. Schulte in 1917 (Bull. Amer. Mus. Nat. Hist. vol. xxxvii. p. 361) listed 21 occurrences, three of which were from New Zealand. There are four skulls, without locality stated (but presumably from Lyall Bay and Petone), in the Dominion Museum, Wellington. Altogether at least 11 specimens have been cast ashore in New Zealand during the past 40 years.

*Napier.*—1892. Skull in Otago Museum.

*Wanganui Beach.*—(a) Skeleton and stuffed skin in the Wanganui Museum. Vertebrae: C. 7, D. 12, L. & Ca. 26 + = 45 +. Cervicals fused. Capitulum of first rib articulates with centrum

of last cervical. Dorsal fin small, falcate. (b) On 3rd February, 1909, I examined at Wanganui a specimen of *Kogia breviceps* which had been stranded at the Heads a few days before. Length, 180 cm.; flipper, 27 cm.; dorsal fin height, 9.5 cm.; distance across flukes, 49 cm. Black above, white below. The accompanying figure was made from a photograph taken at the Heads, where, it was reported, three individuals came ashore. (Pl. II. fig. 3.)

*Cook Strait*.—(a) Port Underwood. Mandible in Dominion Museum, Wellington. Length of ramus, 32 cm.; breadth at angle, 7.5 cm.; symphysis, 6 cm.; width between rami at base, 28.5 cm. Teeth: 14 on right side, 13 on left. (b) Lyall Bay. Cow and calf cast ashore, 1880. (c) Petone, Wellington Harbour. Cow and calf harpooned, 1884. (d) Lyall Bay, 1887. Skeleton in Dominion Museum, Wellington. Teeth 14. 14. Sternum of three segments. Scapula with broad backwardly-directed acromion and shorter and narrowly-directed coracoid, the borders overlapping for the distal half or more. Ribs 12, of which 7 are two-headed. Vertebrae: C. 7, D. 12, L. & Ca. 20 + = 39 +.

*Lyttelton Harbour*.—Female stranded at Governor's Bay, 17th August, 1873. Skeleton and half cast in Canterbury Museum. Exterior and skeleton described by von Haast as the type of *Euphysetes pottsii*. Teeth 13 in each ramus of mandible. Vertebrae: C. 7, D. 12, L. 11, Ca. 20 = 50. Cervicals fused. Ribs 12, of which 6 are two-headed. Sternum of three segments, the first T-shaped. Phalanges: 1, 10, 7, 5, 4.

*Purakanui, Otago*.—Stranded 23rd August, 1900. Skeleton in Cambridge University Zoological Museum. Descriptions by Benham—exterior and skeleton (1902); exterior and anatomy (Proc. Zool. Soc. 1901, p. 107); larynx (Proc. Zool. Soc. 1901, p. 278). Teeth 13 in each ramus of mandible, 1 on each side of upper jaw. Pelvis absent. Vertebrae: C. 7, D. 13, L. 9, Ca. 23 = 52. Ribs 13 pairs, the very last small, 6 are two-headed. Sternum of 3 segments. Phalanges: R. 2, 10, 7, 6, 3; L. 2, 9, 7, 6, 2. (Benham.)

#### BERARDIUS.

*Berardius* Duvernoy, 1851, Ann. Sci. Nat. ser. 3, vol. xv. p. 51; type, *B. arnuxii* Duvernoy.

This genus comprises two species—one from New Zealand and the Argentine, and the other, *B. bairdii*, from the North Pacific.

#### BERARDIUS ARNUXII.

*Berardius arnuxii* Duvernoy, 1851, Ann. Sci. Nat. ser. 3, vol. xv. p. 51 (Akaroa, N.Z.); Gray, 1866, Cat. Seals & Whales Brit. Mus. p. 348; von Haast, 1870, Ann. Mag. Nat. Hist. ser. 4, vol. vi. p. 348; id. 1870, Trans. N.Z. Inst. vol. ii. p. 190; Hector, 1870, Ann. Mag. Nat. Hist. ser. 4, vol. v. p. 222; id. 1873, Trans. N.Z. Inst. vol. v. p. 169; id. 1878, l. c. vol. x. p. 338,



pl. 16; Van Beneden & Gervais, 1880, *Ostéogr. Cét.* pp. 377, 515, Atlas, pl. 21 *bis*, 23, 23 *bis*; True, 1910, *Bull. U.S. Nat. Mus.* 73, p. 68. *Berardius arnouxii* Duvernoy, Flower, 1872, *Trans. Zool. Soc.* vol. viii. p. 212, pls. 27-29; Beddard, 1900, *Book of Whales*, p. 228. "Ziphid Whale," Knox, 1871, *Trans. N.Z. Inst.* vol. iii. p. 125; Hector, 1871, *ib.* p. 129, pls. 16, 17.

The Porpoise Whale has been recorded a number of times in New Zealand and once from La Plata (Marelli, *Ann. Mus. Nac. Buenos Aires*, vol. xxx. p. 411, 1920). The following eleven specimens appear to be all the authentic New Zealand records. Besides these, a whale measured by Knox (1871) at Porirua probably belonged to this species.

*Chatham Island*.—Skull in Otago Museum.

*Coast near Wanganui*.—Skeleton in Wanganui Museum. Skull—length, 115 cm.; mandible, 104 cm. Alveoli two in each ramus. Vertebrae: C. 7, D. 10, L. & Ca. 22+ = 39+. Three cervicals fused. Ribs 10, of which 7 are two-headed, 8th attached to centrum of 7th dorsal, 9th and 10th attached to transverse processes of the corresponding vertebrae. Sternum: 1st and 2nd segments notched in front and behind, 3rd notched in front only; 4th of two lateral pieces, broad in front, united for 6 cm., free and obtusely pointed behind.

*Cook Strait*.—(a) Worser Bay, Wellington Harbour. Stranded January 1870. Skull and other bones in Dominion Museum, Wellington. Measurements of animal given by Knox. Skull described by Hector (1871, 1873). Length of skull, 120 cm. Only one pair of alveoli present in mandible. (b) Entrance to Wellington Harbour. Captured 12th January, 1877. Skeleton in Dominion Museum, Wellington. Exterior and skeleton described by Hector (1878). Teeth two in each ramus of mandible near apex. Vertebrae: C. 7, D. 10, L. 13, Ca. 17 = 47. First three cervicals fused. Ribs 10, of which 8 are two-headed. Sternum of 5 segments. Phalanges: 1, 6, 5, 4, 3.

*Saltwater Creek, north of Banks Peninsula*.—Male, stranded 27th December, 1873. Skeleton in Canterbury Museum. Teeth 2.2. Vertebrae: C. 7, D. 10, L. 13, Ca. 17 = 47. Three cervicals fused. Ribs 10, of which 8 are two-headed. Sternum of four segments. Scapula with broad expanded acromion and narrow thick and but slightly broadening coracoid. Phalanges: 2, 5, 4, 3, 3.

*New Brighton Beach*.—Stranded 16th December, 1868. Skeleton in Museum of Royal College of Surgeons, London. Exterior described by von Haast (1870). Skeleton described by Flower, Van Beneden & Gervais, and Beddard. Vertebrae: C. 7, D. 10, L. 12, Ca. 19 = 48. Three cervicals fused. Ribs 10, of which 7 are two-headed. Phalanges: 2, 5, 4, 4, 3.

*Akaroa*.—(a) 1846. Skull in Paris Museum. Described by Duvernoy as the type of *Berardius arnouxii*. Described and



figured by Van Beneden and Gervais (p. 389, pl. 23). (b) Skeleton in British Museum.

*Otago Peninsula*.—1840. Mandible in Otago Museum. Teeth two in each ramus.

*New Zealand (without locality stated)*.—(a) Skeleton in Paris Museum sent by von Haast. Figured by Van Beneden and Gervais (pls. 21 bis, 23 bis). (b) Skull in U.S. National Museum, Washington. Measurements given by True.

#### MESOPLODON.

*Mesoplodon* Gervais, 1850, Ann. Sci. Nat. ser. 3, vol. xiv. p. 16; type, *Delphinus sowerbensis* Blainville. *Dioplodon* Gervais, 1850, Comptes Rendus, vol. xxxi. p. 512; type, *Delphinus densirostris* Blainville. *Oulodon* von Haast, 1876, Proc. Zool. Soc. 1876, p. 457; type, *Mesoplodon grayi* von Haast. *Dolichodon* Gray, 1866, Cat. Seals & Whales Brit. Mus. p. 353; type, *Ziphius layardi* Gray.

For an account of the species of this genus, see Forbes, Proc. Zool. Soc. 1893, p. 216, and Flower, 1872, Trans. Zool. Soc. vol. viii. p. 211.

MESOPLODON BOWDOINI. (Pl. III. figs. 1-3; Pl. IV. figs. 1-3.)

*Mesoplodon bowdoini* Andrews, 1908, Bull. Amer. Mus. Nat. Hist. vol. xxiv. p. 203, pl. 13 (New Zealand).

This species is now known from two skeletons:—

(1) *New Brighton Beach*.—1904. Skeleton in American Museum of Natural History, New York. Described by Andrews.

Maxillary foramina approximately level with foramina in premaxillaries. Basirostral groove absent. Anterior margin of teeth posterior to hinder edge of mandibular symphysis. Vertebrae: C. 7, D. 10, L. 9, Ca. 20=46. First three cervicals ankylosed. Chevrons 9. Ribs 10, of which 7 are two-headed. Sternum of four segments. Scapula with superior margin of acromion overlapping the coracoid border. Phalanges: 0, 4, 3, 3, 2. (Andrews.)

(2) *New Zealand*.—Skeleton in Dominion Museum, Wellington. This being the second specimen of the species known, a detailed description will be given:—

Skull: Length 72 cm., of rostrum (from outside anteorbital notch) 43.5 cm.; breadth of skull at squamosals 33 cm., at orbits 31.8 cm.; base of rostrum 12 cm. Temporal fossae 9.5 × 6.5 cm. Height from vertex to lower border of pterygoids 30.2 cm., of rostrum at anterior end of pterygoids 8.2 cm. (Pl. III. figs. 1-3.)

Maxillary foramina 3 on right side, 2 on left, about 1 cm. in advance of the premaxillary foramina (1 on each side). Rostrum solid. Contour of upper edge of rostrum straight for two-thirds of its length, then slightly depressed; of lower edge parallel with upper for the first third, then sloping upwards for the middle third, at 14 cm. from apex its height being 5 cm., then gradually narrowing to apex. A prominent ridge on each side of the

expanded portion of the maxillæ curving in anteriorly, and forming the lateral prominences at the base of the rostrum and dividing the anteorbital notches. Proximal ends of premaxillæ strongly everted and overhanging the nares; both directed obliquely backwards, the right 12.5 cm., the left 7 cm. long. Right nasal bone forming the vertex, the left smaller and lower. Mesorostral appearing between the premaxillæ throughout its length; width at rostral base 2.3 cm., at 14 cm. in advance 1 cm., thence widening out towards the distal end. Its proximal end is a thin vertical ridge of bone. Foramen magnum  $5 \times 4$  cm., occipital condyles  $7 \times 4.2$  cm. No basirostral groove. Temporal fossæ pyriform, above the level of the occipital condyles. On the lower surface of the skull the pterygoids diverge, showing the palatines as narrow divergent stripes on each side, about 10 cm. long and 1 cm. wide. Between the palatines the two edges of the maxillæ meet as a median ridge, the bones anteriorly diverging and exposing the vomer. The palatines appear again above the pterygoids, their anterior ends being level with the pterygoid fossæ. Pterygoids broken, but the exterior deeply concave and the basal portion parallel and meeting for a distance of 13 cm.

Mandible: Length of ramus 63 cm., of symphysis 15 cm.; tip to anterior end of left tooth, 13.5 cm.; tooth-line along upper edge of ramus, 11 cm.; width of ramus at posterior end, 12.5 cm.; narrowest portion behind tooth 7 cm., at anterior edge of tooth 6.5 cm. The upper margin curves upwards and slightly outwards (but is not swollen) to form the walls of the alveolus, the internal wall being much higher than the external wall, which in the present specimen falls, but may be broken. (Pl. IV. figs. 1 & 2.)

Tooth: The left tooth only is preserved. Its anterior margin at its junction with the upper edge of the ramus is 15 mm. in advance of the posterior end of the symphysis. Anteriorly the tooth is slightly concave, posteriorly strongly convex. The apex is directed slightly forwards. The base is formed of eight irregular fangs. Anterior margin, 13.8 cm.; base, about 10.5 cm.; thickness, 2.4 cm.

Hyoid bones: Thyrohyals separate; length, 17 cm. Other bones not preserved.

Vertebræ: C. 7, D. 10, L. 9, Ca. 15=41. Atlas, axis, and third cervical fused by both centra and neural arches, 4th and 5th fused only by the neural arch on the right side; 6th and 7th free. Atlas without diapophyses; two conical spines on crest. Diapophyses and parapophyses all separate. Seventh cervical with long diapophyses directed forwards, parapophyses reduced to knobs, above which are the articular facets for the tubercula of the first pair of ribs. Dorsals with centra concave above. Transverse processes of the anterior seven opposite the neural arches and bearing articular facets for the tubercula of the first seven ribs. The first six dorsals bear tubercles on the posterior edges of the centra for the articulation of the capitula of the 2nd to 7th ribs. The 8th, 9th, and 10th dorsals bear short transverse

processes ending in articular facets for the heads of the last three ribs. On the 8th and following vertebræ the transverse processes and metapophyses are widely separated, the former being opposite the centra. Lumbar with strong inferior median carina. Neural spines truncated and expanded at their distal ends. Metapophyses lamellar, projecting forward and upward. Anterior 11 caudals showing facets for chevron bones. The last four are depressed oblong bones with no processes, but there appear to be some missing between the two series. Transverse processes reduced to ridges on the 8th caudal, neural spine rudimentary on the 11th (the 12th and other caudals presumably missing).

Ribs, 10 pairs. The first seven are two-headed, articulating by both capitula and tubercula. The first articulates with the centrum of the 7th cervical and the transverse process of the first dorsal, the 7th articulates with the centrum of the 6th and the transverse process of the 7th dorsal. The 8th, 9th, and 10th are single-headed and articulate with the transverse processes of the 6th to 10th vertebræ. The first two ribs broad and flat, with the proximal ends strongly curved; the remainder with the proximal ends below the articular tubercles roughly triangular or quadrangular in section, the distal ends being flattened.

The greatest length of each rib on the right side in a straight line is as follows:—1st, 30.5 cm.; 2nd, 46.8 cm.; 3rd, 54.7 cm.; 4th, 59.0 cm.; 5th, 60.3 cm.; 6th, 60.4 cm.; 7th, 60.0 cm.; 8th, 55.2 cm.; 9th, 50.5 cm.; 10th, 42.5 cm.

Sternum: The sternum consists of four segments. Three fenestræ are formed at the junctions by notches in the middle of the anterior and posterior margins of the segments. There is a fourth fenestra in the centre of the posterior segment. On each side are five facets for the articulation of the costal ribs—one on the anterior segment, one on the posterior, and one at each of the junctions.

	(1)	(2)	(3)	(4)
	mm.	mm.	mm.	mm.
Greatest length of segments .....	182	116	90	130
Greatest breadth of segments .....	195	130	105	102

Scapula: Breadth, 30.4 cm., length (median), 20 cm. Median length of acromion and coracoid, each about 9 cm. Acromion broad, lamellar projecting upward. Coracoid slender, expanded distally. The superior margin of the acromion is clear of the coracoid border. (Pl. IV. fig. 3.)

Comparison with type of *M. bowdoini*:—The present specimen differs from the type of *M. bowdoini* from New Brighton in no important respect. In the general proportions of the skull and mandible they appear to be within the range of individual variation, and agree in those characters separating *M. bowdoini* as a species: these are the absence of a basirostral groove, short symphysis of mandible, position and size of tooth, relative positions of palatines and pterygoids, overhanging maxillary crest, and

form of the rostrum. On the other hand, the anterior edge of the tooth in the New Brighton specimen is 15 mm. behind the posterior margin of the mandibular symphysis; in the Dominion Museum specimen it is about 14 mm. in advance of it. According to my description, the 8th to 10th dorsal vertebræ have the corresponding ribs articulated to their transverse processes. Andrews states that the 8th rib of *M. bowdoini* is articulated to a facet on the posterior margin of the centrum of the 7th dorsal. The superior margin of the acromion in the type of *M. bowdoini* overlaps the coracoid border, whereas it is clear of it in the present specimen.

#### MESOPLODON GRAYI.

*Mesoplodon grayi* von Haast, Proc. Zool. Soc. 1876, p. 7 (Chatham Island); Flower, 1878, Trans. Zool. Soc. vol. x. p. 417, pls. 71-73; Forbes, 1893, Proc. Zool. Soc. 1893, p. 216, pls. 12-15. *Mesoplodon hectori* (not Gray) Hector, 1874, Trans. N.Z. Inst. vol. vi. p. 86, pl. 15A; id. 1876, l. c. vol. x. p. 339, pl. 17. *Berardius hectori* (not Gray) Hector, 1875, l. c. vol. vii. p. 262. *Oulodon grayi* von Haast, 1876, Proc. Zool. Soc. 1876, p. 457; id. 1877, Trans. N.Z. Inst. vol. ix. p. 450, pl. 26; Van Beneden & Gervais, 1880, Ostéogr. Cét. p. 516, pl. 62. *Mesoplodon haasti* Flower, 1878, Trans. Zool. Soc. vol. x. p. 419, pls. 71, 72. *Mesoplodon australis* Flower, 1878, l. c. p. 419, pls. 71-73; Lillie, 1915, 'Terra Nova' Exped., Zool. vol. i. p. 119. *Mesoplodon knoxi* part (skull B) Hector, 1873, Trans. N.Z. Inst. vol. v. p. 167.

The New Zealand Scamperdown Whale appears to be fairly common in the New Zealand region. Elsewhere it has been recorded only from Patagonia.

*Chatham Islands.*—(a) About 25 individuals stranded on Waitangi Beach, 1875. Three skulls sent to Canterbury Museum. One described by von Haast as the type of *Mesoplodon grayi*. On this specimen von Haast founded the genus *Oulodon*. It has also been described and figured by Forbes. A row of 17 small conical teeth in each side of upper jaw. The two remaining skulls in the Otago Museum. One has 17, the other 19 teeth in each side of the upper jaw. (b) Skeleton in U.S. National Museum, Washington. Vertebræ: C. 7, D. 11, L. 10, Ca. 20=48. Two cervicals fused. Chevrons 9. Ribs 11, of which 7 are two-headed; the last rib rudimentary, about 70 mm. long. (c) Skull and three rostra in British Museum. Described by Forbes. (d) Skeleton in Bishop Museum, Honolulu. Figured in Occ. Papers Bishop Mus. vol. i. no. 5, figs. 4-8, 1902. Ribs 9. Premaxillary behind maxillary foramina.

*North Cape.*—Skeleton found in Great Exhibition Bay, August 1911. Skull and scapula in British Museum. Described by Lillie. Basirostral groove present. Foramina of fifth nerve one behind the other. Height of teeth, 3 in.; length, 2½ in. (Lillie.)



*East Coast, North Island.*—Male stranded, December 1875. Rostrum in Museum of Royal College of Surgeons, London. Described by Flower as the type of *M. haasti*. Measurements given by Forbes. Basirostral groove present. Foramina of fifth nerve one behind the other.

*Cook Strait.*—(a) Lyall Bay. Cast ashore, January 1875. Skeleton in British Museum. Exterior and skeleton described by Hector (1875). Skeleton described by Flower as the type of *M. australis*. Skull measurements given by Forbes. Basirostral groove deep. Vertebrae: C. 7, D. 9, L. 11, Ca. 20=47. Two cervicals united. Ribs 9, of which 7 are two-headed. (Flower.) (b) Wellington. Skeleton in American Museum of Natural History, New York.

*Kaikoura.*—Mandible described and figured by Hector (1874).

*Saltwater Creek, 30 miles north of Banks Peninsula.*—Male stranded 15th December, 1876. Two males and a female stranded 29th December, 1876. Skeleton of one in Canterbury Museum. Skull measurements given by Forbes. Basirostral groove present. Vertebrae: C. 7, D. 10, L. 11, Ca. 19=47. Two cervicals fused. The 8th and 9th caudals are joined by a bony growth. Ribs 10, of which 7 are two-headed. Sternum of 4 segments; 1st large, bifid in front, 2nd and 3rd notched in front and behind, 4th composed of three fused pieces, pointed posteriorly and with a central foramina. Phalanges: 1, 6, 6, 4, 3. Skeleton of another in Museum of Royal College of Surgeons, London. Described by Flower and Forbes. Basirostral groove shallow. Vertebrae: C. 7, D. 10, L. 11, Ca. 20=48. Two cervicals fused. Ribs 10, of which 7 are two-headed. (Flower.)

*Kaiapoi.*—Skull in Canterbury Museum. Described by Hector (1873) and Forbes.

*New Zealand (locality not stated).*—(a) Skull in Otago Museum. Figured by Hector (1878). (b) Skeleton in Paris Museum. Described by Van Beneden and Gervais. Skull measurements given by Forbes. Basirostral groove present. Foramina of fifth nerve one behind the other. 18 teeth in upper jaw on left, 17 on right side. Sternum of 5 segments. Vertebrae: C. 7, D. 10, C. 11, Ca. 19=47. Two cervicals fused. Chevrons 10. Ribs 10, of which 7 are two-headed. Phalanges: 0, 6, 5, 4, 2. (c) Skeleton in Dominion Museum, Wellington. Rostrum narrow, deeper than wide at base. Basirostral groove deep. Foramina of fifth nerve one behind the other. Maxillary large, directed forwards; premaxillary small, behind and directed upwards. Length of skull 75 cm., of rostrum 45 cm.; width at squamosals, 28 cm.; base of rostrum, 5 cm. Mandible length, 67 cm.; symphysis, 21.5 cm. This skull approaches closely the type of *M. australis*. Ribs 10, of which 7 are two-headed. Sternum of 4 segments; the first two free and notched in front and behind, the last two completely fused, the line of junction being denoted by a foramen.



## MESOPLONDON LAYARDI.

*Ziphius layardi* Gray, 1865, Proc. Zool. Soc. 1885, p. 358 (Cape of Good Hope). *Dolichodon layardi* Gray, Hector, 1873, Trans. N.Z. Inst. vol. v. p. 166, pl. 3. *Mesoplodon layardi* Gray, Hector, 1873, Ann. Mag. Nat. Hist. ser. 4, vol. xi. p. 106; id. 1878, Trans. N.Z. Inst. vol. x. p. 341; Flower, 1878, Trans. Zool. Soc. vol. x. p. 416; Turner, 1880, 'Challenger' Rep., Zool. vol. i. pt. 4, p. 2, pls. 1-3; Waite, 1912, Rec. Cant. Mus. vol. i. p. 326, pl. 62; id. 1912, Guide Whales & Dolph. N.Z. p. 16, pl. 4. *Mesoplodon floweri* von Haast, 1876, Proc. Zool. Soc. 1876, p. 478; id. 1877, Trans. N.Z. Inst. vol. ix. p. 442, pls. 25, 26. *Dolichodon traversii* Gray, 1874, Trans. N.Z. Inst. vol. vi. p. 95.

The Strap-toothed Whale has been recorded from South Africa, Australia, and New Zealand.

*Chatham Island*.—Mandible described by Hector (1873) and Turner.

*Great Barrier Island*.—Skull in Canterbury Museum. Teeth meeting over the upper jaw.

*Napier*.—Teeth in Otago Museum.

*Marlborough*.—Skull in Dominion Museum, Wellington; acquired 1879. Length of teeth following curvature, 34 cm.; greatest width, 60 mm. Denticle 7 mm. high, 10 mm. along base-line.

*Saltwater Creek, north of Banks Peninsula*.—Stranded 16th March, 1874. Skeleton in Canterbury Museum. Described by von Haast as the type of *M. floweri*. Vertebrae: C. 7, D. 10, L. 10, Ca. 19=46. Three cervicals fused. Ribs 10, of which 7 are two-headed. Sternum of 4 segments. Scapula with broad acromion and narrow coracoid. Phalanges: 2, 5, 5, 4, 3.

*Lyttelton Harbour*.—Specimen stranded at Allendale, 22nd March, 1912. Half cast in Canterbury Museum. Exterior described by Waite.

*Locality not stated*.—(a) Skull in Dominion Museum, Wellington. Length, 94.5 cm.; breadth, 41 cm.; mandible length, 80 cm.; symphysis, 22 cm. Basirostral groove deep. (Teeth missing.) (b) Skelton in Dominion Museum. Basirostral groove shallow. Length of skull, 61 cm.; of mandible, 52 cm. Vertebrae: C. 7, D. 9, L. 12, Ca. 16=44. Two cervicals fused. Ribs 9, of which 7 are two-headed. Sternum of 3 segments. I have identified this specimen from cranial characters. It is from a young animal, and the teeth are small and triangular. They only differ from those of *M. grayi* in being strongly incurved.

## PAIKEA, gen. n.

I propose this name for those species of Ziphioid Whales with the cranial characters of *Mesoplodon* and two terminal teeth in the lower jaw. Type, *Berardius hectori* Gray. The only other species that can be referred to this genus is *Mesoplodon mirum*.

True, from the North Atlantic. The essential character is the position of the teeth. Other characters which these species have in common are the broad and deep rostrum and the long mandibular symphysis; also, the dorsal fin is placed far back and the teeth completely covered by the gums. In *Mesoplodon*, as it is now proposed to restrict it, the teeth are always placed near the posterior end of the symphysis so that the two species comprising *Paikea* apparently form a natural group in which the teeth, as pointed out by Dr. Harmer (Report Cetacea on British Coasts 1918, p. 21, 1919), possibly correspond with the anterior pair of *Berardius*.

The reduction of the teeth from four to two in the Ziphioid Whales is interesting. *Birardius* is perhaps the most primitive of the recent genera and has usually four teeth, but in a skull in the Dominion Museum, Wellington, only the anterior pair is present. In *Ziphius* and *Hyperoodon* it is the anterior pair that is retained, but in *Mesoplodon* the posterior pair only is present. *Paikea* differs from *Mesoplodon* in possessing only the anterior pair of mandibular teeth.

#### PAIKEA HECTORI.

*Berardius hectori* Gray, 1871, Ann. Mag. Nat. Hist. ser. 4, vol. viii. p. 117; Hector, 1873, Ann. Mag. Nat. Hist. ser. 4, vol. xi. p. 106. *Berardius arnuxii* (not Duvernoy) Hector, 1870, Trans. N.Z. Inst. vol. ii. p. 27. "Ziphid Whale," Knox & Hector, 1871, l. c. vol. iii. p. 125, pls. 14, 15. *Mesoplodon knoxi* Hector, 1873, l. c. vol. v. p. 167. *Mesoplodon hectori* Gray, Flower, 1878, Trans. Zool. Soc. vol. x. p. 416, pls. 71, 72; Forbes, 1893, Proc. Zool. Soc. 1893, p. 227.

Known only from the following specimen:—

*Titahi Bay, Cook Strait*.—Cast ashore January 1866. Skull in British Museum. All the references quoted refer to this specimen. Basirostral groove absent. Foramina of fifth nerve level.

#### ZIPHIUS.

*Ziphius* G. Cuvier, 1823, Ossem. Foss. vol. v. p. 350, pl.; type, *Z. cavirostris* Cuv. *Hypodon* Haldeman, 1841, Proc. Acad. Nat. Sci. Philad. vol. i. p. 127; type, *Delphinus desmaresti* Risso (= *H. cavirostris*).

If *Ziphius* and *Xiphius* be considered variations of the same word, then *Ziphius* Cuvier, 1823, is preoccupied by *Xiphius* Linné, 1758, a genus of fishes, and the next valid name to be used for the genus of whales is *Hypodon* Haldeman, 1841. Professor David Starr Jordan points out to me that *Ziphius* seems to have been purposely so written by Cuvier perhaps to make it clearly different from *Xiphius*, which name was also used by the same author.

## ZIPHIUS CAVIROSTRIS.

*Ziphius cavirostris* G. Cuvier, 1823, Ossem. Foss. vol. v. p. 350 (Mediterranean coast of France); Flower, Proc. Zool. Soc. 1876, p. 477; Hector, 1878, Trans. N.Z. Inst. vol. x. p. 342; Turner, 1880, 'Challenger' Rep., Zool. vol. i. pt. 4, p. 27, pl. 2. *Epidodon chathamensis* Hector, 1873, Ann. Mag. Nat. Hist. ser. 4, vol. xi. p. 105; id. 1873, Trans. N.Z. Inst. vol. v. 164, pls. 4, 5. *Epidodon novæ zealandiæ* von Haast, 1877, Trans. N.Z. Inst. vol. ix. p. 430, pls. 24, 26. *Ziphius novæ zealandiæ* von Haast, 1876, Proc. Zool. Soc. 1876, p. 466; id. 1880, Proc. Zool. Soc. 1880, p. 232; id. 1880, Trans. N.Z. Inst. vol. xii. p. 241, pl. 8. *Ziphius* sp., Scott & Parker, 1889, Trans. Zool. Soc. vol. xii. p. 241, pls. 48-50; Beddard, 1900, Book of Whales, p. 235, pl. 12; Benham, 1901, Proc. Zool. Soc. 1901, vol. i. p. 294. *Hyperoodon planifrons* (not Flower) Waite, 1913, Rec. Cant. Mus. vol. ii. p. 23, pls. 8, 9.

The Goose-beaked Whale has been recorded from all seas.

*Chatham Island*.—(a) Skull in Dominion Museum, Wellington. Described by Hector as the type of *Epidodon chathamensis*. (b) Teeth in British Museum. One figured by Hector, Trans. N.Z. Inst. vol. v. pl. v. figs. 2 a, 2 b.

*East Cape, North Island*.—Teeth and extremity of mandible in Canterbury Museum. Described and figured by Waite, who referred it with doubt to *Hyperoodon planifrons*, but his figure almost matches the anterior end of the mandible of the Petone specimen.

*Cook Strait*.—(a) Near Wellington. Skull described by Turner. (b) Petone Beach, Wellington Harbour. Stranded October 1919. Skeleton in possession of Mr. H. H. Travers, Wellington. Vertebrae: C. 7, D. 9, L. 11, Ca. 19=46. First four cervicals fused, 5th and 6th separately fused by neural arch on left side. Last spinous process and neural canal on the 11th caudal. Ribs 9, of which 6 are two-headed. Sternum of 5 segments, the first 4 are notched in front and behind, the last of two separate lateral pieces. Scapula with long acromion and coracoid.

*Kaiapoi Beach*.—Female, stranded 15th May, 1879. Skeleton in British Museum. Teeth described by von Haast (1880).

*New Brighton Beach*.—Stranded 17th November, 1878. Exterior and teeth described by von Haast (1880).

*Lyttelton Harbour*.—Stranded at Port Cooper, July 1872. Skeleton in Canterbury Museum. Described by von Haast as the type of *Ziphius novæ zealandiæ*. Vertebrae: C. 7, D. 9, L. 11, Ca. 19=46. Four cervicals fused. Ribs 9, of which 7 are two-headed. Sternum of 5 segments, each notched anteriorly and posteriorly. Scapula with long, narrow acromion and coracoid. Phalanges: 2, 5, 5, 4, 3.

*Akaroa Harbour*.—Female, stranded July 1873. Skull described by von Haast (1877).

*Warrington, Otago*.—Came ashore alive, 6th November, 1884. Skeleton in Otago Museum. External characters, skeleton, and

anatomy described by Scott and Parker; larynx described by Benham. Two sharp-pointed teeth at apex of mandible. Vertebrae: C. 7, D. 10, L. 9, Ca. 20=46. Four cervicals fused. Ribs 10, of which 7 are two-headed. Sternum of 5 segments, each notched in front and behind. Pelvic bones about 9 cm. long. Phalanges: 1, 5, 5, 5, 2.

*Locality not stated.*—Skull of young in British Museum.

#### ORCINUS.

*Orcinus* Fitzinger, 1860, Wiss.-populäre Naturg. Säug. vol. vi. p. 204; type, *O. orca* (= *Delphinus orca* Linné). (*Orca* Gray, 1846, is preoccupied by *Orca* Wagler, 1830, a genus of Phyepteridæ.)

#### ORCINUS ORCA.

*Delphinus orca* Linné, 1758, Syst. Nat. ed. 10, p. 77 (European seas). *Orca gladiator* Gray, 1846, Zool. 'Erebus' & 'Terror,' p. 33; Hector, 1885, Trans. N.Z. Inst. vol. xvii. p. 208. *Orca pacifica* Gray, Hector, 1875, l. c. vol. vii. p. 260.

The Killer Whale is found in all seas. Lillie has recorded it as far south as McMurdo Sound, and states that it is the commonest cetacean in the Ross Sea. It is occasionally seen off the New Zealand coast, especially about Cook Strait. Besides the following definite records, there is a skull of unknown locality in the Auckland Museum.

*Chatham Island.*—Skull in Canterbury Museum. Teeth  $\frac{11}{13}$ .

*Coast south of Wanganui.*—Skeleton in Dominion Museum, Wellington. Vertebrae: C. 7, D. 11, L. 10, Ca. 24 = 52. Four cervicals fused; 5th and 6th separately fused by neural arches only. Teeth  $\frac{11}{12}$ . Ribs 11, of which 6 are two-headed. Sternum of one piece with five articular facets on each side.

*Otago Heads.*—Skull in Otago Museum. Described by Hector (1875). Teeth  $\frac{12}{12}$ .

#### PSEUDORCA.

*Pseudorca* Reinhardt, 1862, Overs. K. Danske Vidensk. Selsk. Forhandl. p. 151; type, *P. crassidens* (= *Phocæna crassidens* Owen).

#### PSEUDORCA CRASSIDENS.

*Pseudorca crassidens* Owen, 1846, Brit. Foss. Mamm. p. 516 (North Sea). *Pseudorca meridionalis* Flower, Hector, 1873, Trans. N.Z. Inst. vol. v. p. 163.

The range of this species, which may be called the Tasmanian Blackfish, extends from the North Sea to the Chatham Islands. It is met with in large schools in New Zealand and Tasmanian waters.



*Chatham Island*.—In March 1906 a school of several hundreds was stranded on Long Beach, Petre Bay. These were referred to by Waite (Subant. Is. N.Z. p. 551, under *Globiocephalus melas*), who visited the locality in February 1907. In December 1909 the remains of many of them were still to be seen, and I was able to identify the species as *Pseudorca crassidens*. Teeth in upper jaw 8 on each side.

*Lyll Bay*.—Cranium in Dominion Museum, Wellington. Described by Hector. This was at one time referred by Hector to *Beluga* (Ann. Mag. Nat. Hist. ser. 4, vol. ix. p. 438, 1872).

#### GLOBICEPHALA.

*Globicephala* Lesson, 1828, Hist. Nat. Mamm. et Ois. vol. i. p. 441; type, *Delphinus deductor* Scoresby (= *D. melas* Traill).

#### GLOBICEPHALA MELÆNA.

*Delphinus melas* Traill, 1809, Nicholson's Journ. vol. xxii. p. 21 (North Atlantic). *Globiocephalus macrorhynchus* Gray, Hector, 1870, Trans. N.Z. Inst. vol. ii. p. 28; id. 1873, l. c. vol. v. p. 164; id. 1875, l. c. vol. vii. p. 261, pls. 16, 16 A; id. 1877, l. c. vol. ix. p. 481, pls. 13, 13 A; id. 1870, Ann. Mag. Nat. Hist. ser. 4, vol. v. p. 222. *Globicephalus melas* Traill, Hector, 1885, Trans. N.Z. Inst. vol. xvii. p. 209; Waite, 1909, Subant. Is. N.Z. p. 551.

The Blackfish is found in all tropical and temperate seas. Like its relative the Tasmanian Blackfish, it goes about in schools. It is occasionally reported stranded in considerable numbers, but as the term "blackfish" is popularly applied to several species, the specific identity is not always certain. Skeletons and skulls are common in New Zealand museums.

*Chatham Islands*.—Skull in Dominion Museum, Wellington (according to Hector, Ann. Mag. Nat. Hist. ser. 4, vol. xi. p. 105, 1873).

*Cook Strait*.—(a) Two skulls and other bones in the Dominion Museum. Described by Hector (1870, p. 28; 1873). One of the skulls is very massive, measuring 67.5 cm. in length and 47.5 cm. in breadth. Rostrum: length, 34 cm.; breadth at base, 26.5 cm. Pterygoids approximating to within 3 or 4 mm. Teeth  $\frac{9}{5}$ . Intermaxillaries broad, expanding a little in front, approaching to within 2 cm. of the edge of the maxillaries, upper surface rugose anteriorly. Six cervical vertebræ fused. (b) *Lyll Bay*. School ran ashore, January 1876. Ten skeletons were secured. One now mounted in Dominion Museum. Exterior of animal and skeleton described by Hector (1877). Teeth  $\frac{10}{9}$ . Vertebræ: C. 7, D. 11, L. 13, Ca. 29=60. Six cervicals fused. Ribs 11, of which 7 are two-headed. Phalanges: 4, 13, 10, 3, 1. Two skeletons in the British Museum are perhaps from this school. (c) Skeleton in Otago Museum. Teeth  $\frac{9}{10}$ . Vertebræ: C. 7, D. 11, L. 12, Ca. 26=56. Four cervicals fused. Ribs 11, of which 6 are



two-headed. Sternum of 3 segments, the first two perforated, the last divided longitudinally.

*Otago*.—Skeleton in Canterbury Museum. Pterygoids separated along the middle line of about 1 cm. Teeth  $\frac{10}{10}$ . Vertebrae: C. 7, D. 11, L. 14, Ca. 24 = 56. Six cervicals fused. Pelvic bones curved, rod-like, about 15 cm. long. Ribs 11, of which 6 are two-headed. Sternum of 3 segments, the anterior one notched in front, perforated in the centre, and with the sides projecting outwards and backwards. Scapula with broad L-shaped acromion, coracoid with distal end expanded.

*Stewart Island*.—(a) Skull in Otago Museum. (b) Captured January 1874. Skeleton in British Museum, exterior described by Hector (1875).

*Campbell Island*.—(Filhol, Mission d'Ile Campbell, Zool. p. 34, 1885, *G. macrorhynchus*).

*Locality not stated*.—(a) Skull in Auckland Museum. Figured by Hector (1875, pl. 16). (b) Skeleton in Dominion Museum. Teeth  $\frac{8}{8}$ . Vertebrae: C. 7, D. 11, L. 13, Ca. 25 = 56. Five cervicals fused. Ribs 11, of which 6 are two-headed. Sternum of 3 segments.

#### GRAMPUS.

*Grampus* (§ *Delphinus*) Gray, 1828, Spicilegia Zoologica, vol. i. p. 2; type, *Delphinus griseus* Cuvier.

#### GRAMPUS GRISEUS.

*Delphinus griseus* Cuvier, 1812, Ann. Mus. vol. xix. p. 14 (Brest, France). *Grampus richardsoni* Gray, Hector, 1873, Trans. N.Z. Inst. vol. v. p. 163. *Grampus griseus* Cuv., Waite, 1912, Rec. Cant. Mus. vol. i. p. 328, pl. 63; id. 1912, Guide Whales & Dolph. N.Z. p. 19, pl. 5.

Risso's Dolphin has been recorded in such widely sundered regions as the North Sea and the coast of New Zealand. It is a rare species wherever found. Only twice has it been recorded from our seas.

(1) *Manawatu Beach*.—Mandible in Dominion Museum, Wellington. Described by Hector. Length of ramus 44.5 cm., of symphysis 6 cm. Teeth 3 on each side opposite the symphysis, blunt, conical, the posterior one 8 mm. in diameter and projecting 8 mm. above the dried gum.

(2) *Pelorus Sound*.—Figured by Waite. It is strange that the famous cetacean known as "Pelorus Jack" should not have been mentioned in scientific literature until Waite in a short note confirmed the identification of the Rev. D. C. Bates, and published a photograph showing the contour of the dorsal fin and flukes. It has an extensive literature in newspapers and magazines. A special booklet by J. Cowan has been devoted to it, while an article on "Pelorus Jack—Tuni-Rangi," by W. T. Downes, appears in the Journal of the Polynesian Society, vol. xxiii. p. 176, 1914. Both these give the Maori legend.

"Pelorus Jack" has been described as "bluish-white tinged with yellow and purple, and with irregular brown-edged scratch-like lines in all directions. His flippers are blackish and mottled with grey" (Cowan). Length about 14 ft. Dorsal fin high and falcate. This famous cetacean for many years frequented the waters outside the entrance to Pelorus Sound, and was in the habit of meeting steamers on the route between Nelson and Wellington. It accompanied the vessels for some miles, and played from side to side of the bows, keeping just in front and frequently leaping out of the water. It was protected by an Order in Council. "Pelorus Jack" has not been seen since 1912.

#### CEPHALORHYNCHUS.

*Cephalorhynchus* (§ *Delphinus*) Gray, 1846, Zool. 'Erebus' & 'Terror,' Mamm. p. 36; type, *D. heavisidii* Gray.

#### CEPHALORHYNCHUS HECTORI. (Pl. II, figs. 1 & 2.)

*Electra hectori* Van Beneden, 1881, Bull. Roy. Acad. Belg. ser. 3, vol. i. p. 887, pl. 2. *Lagenorhynchus clangulus* (not Gray) Hector, 1870, Trans. N.Z. Inst. vol. ii. p. 27; id. 1872, Ann. Mag. Nat. Hist. ser. 4, vol. ix. p. 436, fig. *Electra clangula* (not Gray) Hector, 1873, Trans. N.Z. Inst. vol. v. p. 160, pl. 12; id. 1877, l. c. vol. ix. p. 350, pl. 11. *Cephalorhynchus hectori* Ben., Hector, 1885, Trans. N.Z. Inst. vol. xvii. p. 209; True, 1889, Bull. U.S. Nat. Mus. xxxvi. pp. 112, 177, pl. 32. *Cephalorhynchus albifrons* True, 1899, l. c. pp. 111, 177, pl. 32.

Confined to New Zealand seas. It is the Common White-nosed Porpoise, never seen far from the coast.

*North Coast*.—Specimen captured. Skeleton in Paris Museum. Described by Van Beneden as the type of *Electra hectori*. Teeth 30. Vertebrae: C. 7, D. 14, L. 15, Ca. 27=63. Two cervicals fused. Ribs 14.

*Bay of Islands*.—Skull in Dominion Museum. Teeth 30. Length of skull 30.5 cm., of rostrum 14.5 cm.; width of rostrum at base, 7.5 cm.

*Wanganui Coast*.—(a) Skeleton in Wanganui Museum. Sternum of two segments; four pairs of ribs articulate with the anterior and one pair with the posterior segment, which is perforated. Two cervicals fused. (b) Stuffed skin in Wanganui Museum. Specimen stranded alive, Castlecliff Beach, May 1921. Mr. G. Shepherd, Curator of the Wanganui Museum, has kindly supplied me with a description which enables me to give the following particulars. Forehead grey. Snout and a margin round the grey of the forehead, black. Dorsal surface slaty black, shading into slaty grey on the sides and then into black bordering the white under surface. Tip of lower jaw, flippers, dorsal fin, and tail black. A white spot in the axil of each flipper. Under surface white, interrupted by an isthmus of black connecting the two flippers. The white extends backwards to midway between

the vent and the flukes, dividing into three equally long pointed (Pl. II. figs. 1 & 2) bands, one central and one extending obliquely along each flank. An elongated dusky patch surrounds the vent. Total length of specimen 1.90 m. An interesting point to observe is that, according to Mr. Shepherd, the forehead is grey and not white. This intermediate colour probably accounts for the varying descriptions given to this animal, resulting in it having been listed under two names.

*Cook Strait*.—(a) Outside Wellington Harbour. Described by Hector (1870). Vertebrae: C. 7, D. 14, L. & Ca. 48=69. (b) Off Cape Campbell. Two shot from a large school. Exterior described by Hector (1872, 1873). (c) Wellington Harbour. Skull in Dominion Museum. Teeth  $\frac{31}{2}$ . Length of skull 31.2 cm., of rostrum 16 cm.; width of skull at squamosals 16 cm., of rostrum at base 8 cm. (d) Half model in Otago Museum. There is also a skeleton, perhaps of this specimen, but locality not given.

*Canterbury*.—(a) Skeleton from Banks Peninsula in Canterbury Museum. Vertebrae: C. 7, D. 13, L. 15, Ca. 29=64. Two cervicals fused. Ribs 13, of which 4 are two-headed, last rib less than half the length of the 12th. Sternum of one piece. (b) Skull in U.S. National Museum, Washington.

#### LAGENORHYNCHUS.

*Lagenorhynchus* Gray, 1846, Zool. 'Erebus' & 'Terror,' Mamm. p. 30; type, *Delphinus acutus* Gray.

#### LAGENORHYNCHUS OBSCURUS.

*Delphinus obscurus* Gray, 1828, Spic. Zool. p. 2 (Cape of Good Hope). *Clymenia obscura* Gray, Hector, 1873, Trans. N.Z. Inst. vol. v. p. 160, pl. 1; id. 1877, l. c. vol. ix. pl. 11; id. 1885, l. c. vol. xvii. p. 211; Hutton, 1877, l. c. vol. ix. p. 349.

The Dusky Dolphin is common round the coast. It is apparently widely distributed, being recorded from the Cape seas and in the Southern Ocean as far south as 58° S. lat. (Lillie.)

*Wanganui Coast*.—(a) Skull in Dominion Museum, Wellington. Described by Hector (1873). Teeth  $\frac{34}{2}$ . Length of skull, 35.5 cm.; breadth at squamosals, 16.7 cm.; rostrum length, 19.3 cm.; breadth at base, 8.5 cm. (b) Two specimens in Wanganui Museum.

*Cook Strait*.—Skeleton in Dominion Museum. Teeth  $\frac{30}{2}$ . Vertebrae: C. 7, D. 13, L. 19, Ca. 32=71. Two cervicals fused. Ribs 13, of which 6 are two-headed. Phalanges: 2, 9, 6, 2, 1. Sternum of 3 segments.

*Banks Peninsula*.—(a) Lyttelton Harbour. Skull in Canterbury Museum. (b) Akaroa. Cast in Canterbury Museum.

There are two other skeletons of unknown locality in the Dominion Museum.

## LISSODELPHIS.

*Lissodelphis* Gloger, 1841, Hand- u. Hilfsb. Naturg. vol. i. pp. xxxiv, 169; type, *Delphinus peronii* Lacépède. (*Tursio* Wagler, 1830, is preoccupied by *Tursio* Fleming, 1822, a genus of Physteridæ.)

## LISSODELPHIS PERONII.

*Delphinus peronii* Lacépède, 1804, Hist. Nat. Cét. p. 316 (south of Tasmania). *Tursio peronii* Lacép., Lillie, 1915, 'Terra Nova' Exped., Zool. vol. i. p. 121.

This species is included in the New Zealand fauna on the authority of Lillie, who records seeing two specimens in lat. S. 47° 04', long. E. 171° 33' (south-east of Nugget Point, Otago). The species is easily recognised on account of its peculiar coloration. It has been recorded in the Southern Ocean from Tasmania to Chile.

## STENELLA.

*Stenella* (§ *Steno*) Gray, 1866, Proc. Zool. Soc. 1866, p. 213; type, *Steno attenuatus* Gray. *Prodelphinus* Gervais, 1880, Ostéogr. Cét. p. 604; type, *P. marginatus* Duvernoy (= *P. euphrosyne* Gray).

I have adopted *Stenella* as the earliest valid name for this genus, passing over *Sousa*, proposed earlier on the same page, because it is probably only a variation of *Susu* (preoccupied by Lesson, 1828). It may also be added that *Susu* or *Sousou* is a Hindu word, and therefore the type of *Sousa*, if not hitherto fixed, should be the Indian species *S. lentiginosus*.

## STENELLA EUPHROSYNÆ.

*Delphinus euphrosyne* Gray, 1846, Zool. 'Erebus' & 'Terror,' p. 40, pl. 22. *Clymenia novæ zealandiæ* (not Quoy & Gaimard) Hector, 1873, Trans. N.Z. Inst. vol. v. p. 159, pl. 2; id. 1877, l. c. vol. ix. pl. 11.

A large species, recorded from the North and South Atlantic. Its claim to be included in the New Zealand fauna rests on the following skull:—

*Waikanae Coast*.—Skull in Dominion Museum, Wellington. Described and figured by Hector. The proportions of this skull and the position of the nerve foramina agree with the type of *D. euphrosyne* as figured by Gray (Zool. 'Erebus' & 'Terror,' pl. 22). Teeth  $\frac{43+}{45}$ . Length of skull 48 cm., of rostrum 28.4 cm.; breadth of skull at squamosals, 23.3 cm.; breadth of rostrum at base, 12 cm. Pterygoids approximate to within 2 mm.



## STENELLA PSEUDODELPHIS.

*Delphinus pseudodelphis* Schlegel, 1841, Abhandl. Gebiete Zool. Heft 1, p. 22. *Clymenia attenuata* Gray, Hector, 1885, Trans. N.Z. Inst. vol. xvii. p. 211.

This Dolphin has been recorded from the South Atlantic Ocean and Cape seas. Probably it should be united with *S. malayanus* Lesson (1826) and *S. frenatus* F. Cuvier (1836), and the distribution given as Atlantic, Indian, and Pacific Oceans. Its inclusion in the New Zealand fauna rests on a single skull. There is also in the Dominion Museum a mandible which I refer to this species. The tip is broken, but there are 36 alveoli present. Length of ramus 34 cm., of symphysis 6 cm.

*Parapara*.—Skull in Dominion Museum. Hector doubted this skull being obtained in the New Zealand area. It, however, bears the legend "Loc. Parapara. Hector 1879. *Steno attenuatus* Gray" written on the premaxillæ. The proportions of the skull and the contour of the premaxillæ are identical with the type of *D. attenuatus* figured by Gray (Zool. 'Erebus' & 'Terror,' pl. 28), but there are high fronto-supraoccipital ridges (like the figure of *D. doris* in Gray's work). It is a large skull, and the high ridges may be a sign of age. Pterygoids in contact. Teeth missing, alveoli 39, but end of rostrum not quite perfect. Length of skull 39.2 cm., of rostrum 24 cm.; breadth of skull at squamosals 16.2 cm., at orbits 14.7 cm.; breadth of rostrum at base 9 cm.

## DELPHINUS.

*Delphinus* Linné, 1758, Syst. Nat. ed. 10, p. 77; type, *D. delphis* Linné.

## DELPHINUS DELPHIS.

*Delphinus delphis* Linné, 1758, Syst. Nat. ed. 10, p. 77 (European seas). *Delphinus novæ zealandiæ* Quoy & Gaimard, 1830, Voy. 'Astrolabe,' Zool. vol. i. p. 149, pl. 28; Hutton, 1877, Trans. N.Z. Inst. vol. ix. p. 349. *Delphinus forsteri* Gray, Hector, 1872, Ann. Mag. Nat. Hist. ser. 4, vol. ix. p. 438; id. 1873, Trans. N.Z. Inst. vol. v. p. 158, pls. 2, 3; id. 1874, l. c. vol. vi. p. 85; id. 1877, l. c. vol. ix. pl. 11.

The Dolphin is found in all seas; it is common round the New Zealand coasts.

*Bay of Islands*.—Skull in Dominion Museum.

*Hauraki Gulf*.—I have seen a skull from Motutapu Island.

*East Coast, North Island*.—Specimen captured by the 'Astrolabe' off Tolaga Bay. Described by Quoy and Gaimard as the type of *Delphinus novæ zealandiæ*.

*Wanganui Beach*.—Skull described by Hector (1873).

*Cook Strait*.—(a) Lyall Bay. Skeleton in Dominion Museum. Exterior described by Hector (1874). Teeth  $\frac{48}{48}$ . Vertebrae: C. 7, D. 14, L. 17, Ca. 37=75. Two cervicals fused. Ribs 14,



of which 3 are two-headed. Costal ribs 8, of which 5 articulate with the sternum. Sternum of one piece. Phalanges : 2, 9, 7, 2, 1. (b) *Porirua*. Skull in Dominion Museum. Described by Hector (1872).

*Lyttelton Harbour*.—Skeleton in Canterbury Museum, from Governor's Bay, 1896. Vertebrae : C. 7, D. 15, L. 20, Ca. 33=75. Ribs 15, of which 5 are two-headed, the last pair small, half the length of the 14th. Costal ribs 8, of which 4 appear to articulate directly with the sternum. Sternum of one piece, apparently of three fused segments. Pelvic bones curved, rod-like, about 8 cm. long.

There is a skeleton from New Zealand in the British Museum. True (Bull. U.S. Nat. Mus. 36, p. xxxvi, 1889) gives the measurements of the skull.

### TURSIOPS.

*Tursiops* Gervais, 1855, Hist. Nat. Mamm. vol. ii. p. 323; type, *Delphinus tursio* Fabricius (= *D. truncatus* Montagu).

### TURSIOPS TRUNCATUS.

*Delphinus truncatus* Montagu, 1815, Wern. Trans. vol. iii. pl. 5. *Tursio metis* Gray, Hector, 1873, Trans. N.Z. Inst. vol. v. p. 162; id. 1877, l. c. vol. ix. p. 477, pls. 11, 12; Hutton, 1876, l. c. vol. viii. p. 180. *Tursiops tursio* (Fabr.), Hector, 1885, l. c. vol. xvii. p. 210. *Beluga kingii* (not Gray) Hector, 1873, Ann. Mag. Nat. Hist. ser. 4, vol. xi. p. 105; id. 1873, Trans. N.Z. Inst. vol. v. p. 163. *Delphinapterus leucas* (not Pallas) Hector, 1885, l. c. vol. xvii. p. 209.

The Cowfish appears to be widely distributed, having been recorded from localities as distant as the North Sea and New Zealand. In the latter place it has been recorded from both east and west coasts of the South Island.

*Lyttelton Harbour*.—Skeleton in Canterbury Museum, from Governors Bay, 1895. Teeth  $\frac{21}{20}$ . Vertebrae : C. 7, D. 13, L. 17, Ca. 27=64. Two cervicals fused. Ribs 13, with a vestige about 4 cm. long on the right side only of a 14th. Costal ribs 9, of which the first is rather broad and thick, five articulate directly and four indirectly with the sternum. Sternum of 4 segments, the anterior curved upwards and notched in front and with a minute perforation in the centre.

*Otago Harbour*.—1913. Skull and cast in Otago Museum.

*Dusky Sound*.—(a) Skull in Otago Museum. 1898. (b) Skeleton in Otago Museum. Captured in Useless Bay, 10th May, 1875. Exterior and skull described by Hutton. Teeth  $\frac{23}{22}$ . (c) Skeleton in Dominion Museum. Captured in Useless Bay, 10th May, 1875. Described by Hector (1877). Teeth  $\frac{23}{23}$ . The anterior pair, upper and lower small, not projecting above the alveoli. Vertebrae : C. 7, D. 12, L. 17, Ca. 28=64. Two cervicals fused. Ribs 12, of which 4 are two-headed. Costal ribs 10, of which 5 articulate

with the sternum. Sternum of 4 fused segments. (*d*) Skull in Dominion Museum, labelled "Dusky Bay, 6/1/73."

*Locality not stated.*—(*a*) Skeleton in Wanganui Museum. Teeth  $\frac{22}{6}$ . Vertebrae: C. 7, D. 12, L. 17, Ca. 22 + = 58 +. Ribs 12, of which 5 are two-headed. Two cervicals fused. (*b*) Skull (incomplete) in Dominion Museum. Labelled in Dr. Knox's handwriting "*Beluga kingii* Gray. The Australian Beluga. From Swainson Coll." This is merely an imperfect cranium; the whole of the rostrum and mandible are missing. It is from a young animal, as the frontal is quite separate and the cranial sutures are open. It appears to agree in all essential characters with the skulls of *Tursiops truncatus* in the Dominion Museum. The main point of difference which gives the present specimen a distinct appearance is the absence of a transverse supraoccipital ridge, but this is obviously due to age, and could not be expected to be pronounced in a young animal. This specimen was referred to under the name *Beluga kingii* by Hector (1873), and is responsible for the introduction into New Zealand literature of the "White Whale, *Delphinapterus leucas*," which finds a place in Hutton and Drummond's 'Animals of New Zealand,' but has been treated more cautiously by Waite, who omitted it altogether in his 'Guide to the Whales and Dolphins of New Zealand.'

#### EXPLANATION OF THE PLATES.

##### PLATE I.

###### *Neobalæna marginata.*

- Fig. 1. Skull, lateral view.  
2. Skull, superior view.  
3. Skull, inferior view.

##### PLATE II.

###### *Cephalorhynchus hectori.*

- Fig. 1. Side view.  
2. Inferior view.

###### *Kogia breviceps.*

- Fig. 3. Specimen stranded at Wanganui,  
February 1909.

##### PLATE III.

###### *Mesoplodon bowdoini.*

- Fig. 1. Skull, superior view.  
2. Skull, inferior view.  
3. Skull, lateral view.

##### PLATE IV.

###### *Mesoplodon bowdoini.*

- Fig. 1. Mandible.  
2. Left ramus of mandible.  
3. Scapula.



29. On the Dental Characters of certain Australian Rats.  
By Prof. F. WOOD JONES, Adelaide University.

[Received May 22, 1922 : Read June 13, 1922.]

(Text-figures 1-12.)

The observations recorded in the present paper, although very limited in their scope, may possibly prove to be of some value when they are extended over a wider range of types than is available to the author.

The business of diagnosing the specific characters of the material which he studies does not, as a rule, fall within the province of the anatomist, but there are times when even the teacher of human anatomy has to enlarge his field of enquiry, and enlarge it so that he comes within measurable distance of being a systematic zoologist. The attempt to assign a specific name to an Australian Murine is an enterprise no amateur should engage in, and it must not be thought that the present author is responsible for the determination of the species mentioned here. But short of giving an actual name to a species, it may happen that one who is not a systematic zoologist may want to track down, as nearly as possible to its proper position, some animal into the structure of which he is enquiring.

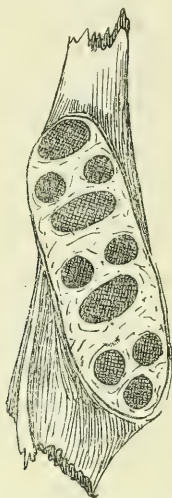
Among the characters which bulk large in the differential diagnosis of various Murines are the crown patterns of the molar teeth. It is quite certain that not a tithe of the literature dealing with the molar patterns of the rats has been reviewed during a search of the works and periodicals available here in Adelaide; but enough has been studied to convince the author that although it is a simple thing to diagnose the crown occlusal pattern of the molars of a young animal, it is difficult or even impossible to say what may have been the pattern when once the molars are worn down in an old or an aged specimen. Text-fig. 8 illustrates the condition of the left upper molar series in three individuals belonging to one species, and it is easy to see that in the oldest individual a diagnosis of the original occlusal pattern is a matter of considerable uncertainty. Consideration of the interesting problem of the relation of crown-pattern to root-formation has prompted the author to turn to the root-patterns in order to see if they presented any constant or useful features.

A series of circumstances has led up to this little investigation of the root-patterns of a few Australian rats. In the first place, a number of skulls and certain cranial fragments were found upon an island,—Franklin Island in Nyct's Archipelago,—the living rats inhabiting which had been already properly identified. The skulls were all of aged individuals, and no diagnosis could be made from the molar patterns; and yet it was of some importance that the identity of the fragments should be sufficiently well

established to make their relation to the living rats of the island clear.

In the next place, upon another island (Goat Island) in the same Archipelago the tracks of a rat were seen upon the sea-beaches, but despite every effort no rat could be caught or shot or even seen during a brief visit to the island. Nevertheless the fact that the tracks were in reality those of rats was proved by the finding of skull fragments in the dejecta of some birds of prey. These fragments were all of lower jaws and lacked teeth (see text-fig. 1). Save for a single humerus no other portion of the rats was recovered. It was a matter of some interest to see if the rat of Goat Island, and the living rat of Franklin Island, and the dead rat of Franklin Island were or were not identical.

Text-figure 1.



Fragment of left lower jaw taken from the pellets of birds of prey on Goat Island, Nuyt's Archipelago. The edentulous alveolus has a characteristic root-pattern.

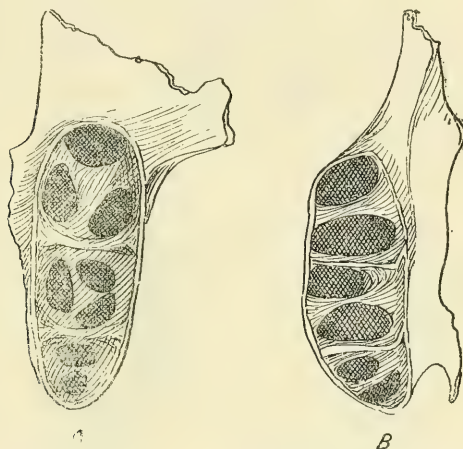
Still more recently the author was confronted with the remains of so many rats that the deposit formed by their bones constituted so vast a bulk as to be exploited as a commercial undertaking, though situated some 40 miles from the railroad and some 200 miles from the place to which the deposit could be sent by rail. These bones were in a system of caves (Buckalowie), and among the millions of rats which had gone to the formation of the deposit not one seems to be represented by a whole skull. Jaws and fragments of jaws devoid of teeth were to be had by the thousand (see text-fig. 2), and at once the question arose—Could the fragments be identified by an examination of the jaws from which the teeth had been lost? Whatever the rats were,



they were certainly ancient and they were mixed with the remains of many other animals, amongst which were *Thylacinus* and *Thylacoleo*. Even the accident of the loss of teeth in the jaw fragments composing the deposit on the floor of the caves provided a partial answer to the question, for it was at once evident from an examination of the alveolar cavities for the upper molars that two quite different root-patterns were represented.

In order to determine the affinities of these root-patterns the author extracted teeth from such properly identified skulls as he could obtain, and the present paper is merely a record of the findings. If the results are capable of no further extension, at least they permit one to say that the past and present rats of

Text-figure 2.



Typical fragments from bone debris of Buckalowie Cave deposit. A. Portion bearing left upper molar root-cavities. B. Left lower molar root-cavities.

Franklin Island are the same animal, that the murine contemporary of *Thylacoleo* which formed the cave-deposit at Buckalowie, was a creature a good deal like the Franklin Island rat; but that the unknown rat which lives on Goat Island is not the same sort of rat at all, but is like a rat whose remains make a small and recent addition to the cave-deposits and like existing members of the genus *Rattus*.

#### HYDROMYS Geoff., 1805.

The species examined is that known as the "Golden-bellied Water-Rat," *H. chrysogaster* Geoff. It is now a comparatively rare animal, and in South Australia (and in some of the other States) it is becoming increasingly difficult to obtain. The specimens examined were trapped either on the Onkaparinga River in the Mount Lofty Range or on the River Murray at Tailem Bend. The animal is so thoroughly distinctive that its specific diagnosis needs no authority.

*Upper Molars.*

The upper molar series when examined from its occlusal surface presents a remarkably simple pattern in the young animal when practically no signs of attrition are present, and the same simplicity is preserved in the adult when attrition is well advanced (see text-fig. 3, A). The anterior molar consists of three very distinct masses arranged in the antero-posterior axis of the tooth.

Text-figure 3.



Left upper molar series of *Hydromys chrysogaster*. A, showing the occlusal surface of the two molars; and B, the alveolar cavities. The outlines of the anterior molar are superimposed on its alveolar cavities in B. The cavity marked X is not present in some specimens.

Each of these divisions shows a central depressed area when viewed from the occlusal surface.

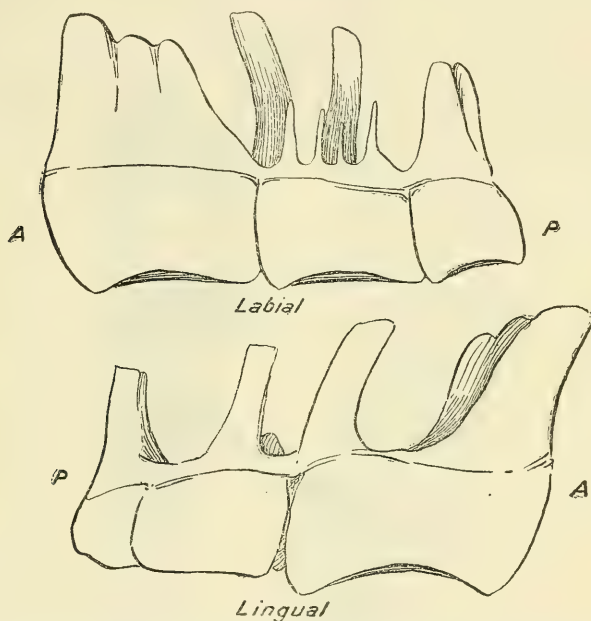
The posterior molar consists of a small anterior lingual portion and a larger posterior mass. The total area of the posterior molar is less than half that of the anterior tooth. (See text-fig. 3.) In advanced age the wear of the tooth involves the raised rim of the individual crown masses, and beyond a flattening of

the occlusal surfaces no marked change of crown-pattern takes place with increasing age.

Upon removing the two upper molars in *Hydromys* a very curious arrangement of the alveolar cavities is seen. There are either 8 or 9 separate sockets for the reception of roots, small or large, of the anterior tooth, and two cavities for the roots of the posterior tooth. (See text-fig. 3, B.)

Of the 8 or 9 root-cavities for the anterior tooth 2 belong to the anterior lamina of the crown, 5 or 6 belong to the middle lamina, and 1 to the posterior lamina.

Text-figure 4.



Anterior left upper molar of *Hydromys chrysogaster* to show the relation of the multiple roots to the crown divisions. In this example only two lingual roots are present. A=anterior, P=posterior extremity of molar.

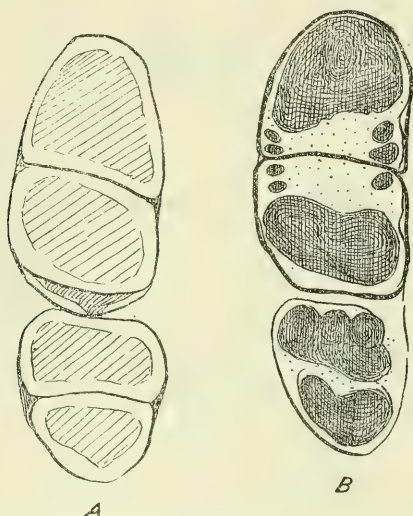
The anterior root is large and shows at its extremity a tendency to be itself subdivided into 3. Four very minute labial cavities belong to four small labial roots of the medial lamina and one or two far larger lingual root-cavities belong to the same subdivision. The small posterior portion of the anterior molar has one large alveolus for a single large root which shows a marked tendency to be bifid. (See text-figs. 3 & 4.)

The two roots of the posterior tooth are arranged in the long axis of the jaw and thus both tend to be elongated from side to side and to be bifid.

*Lower Molars.*

The lower molar series consists of two dental masses with the same simple type of occlusal surface as that displayed by the upper teeth. The anterior molar is divided into two main parts, and in some specimens, but not in all, a very small posterior shelf is present. The posterior molar is also divided into two main masses, but the whole area of the tooth is considerably less than that of the anterior one. (See text-fig. 5, A.) Again there is the same complexity of the alveolar cavities and roots. Again 9 root-cavities belong to the anterior molar mass. The anterior portion of the anterior molar has a large anterior root and two

Text-figure 5.



Left lower molar series of *Hydromys chrysogaster*. A. Occlusal surface.

B. Alveolar cavities, the outlines of the anterior molar being shown.

small postero-lingual and two small postero-labial roots. The posterior portion has two small labial, one small lingual, and a large, transverse, and partially sub-divided posterior root. There are again two rather tortuous root-cavities, situated antero-posteriorly, for the posterior molar. (See text-fig. 5, B.)

Looking at the whole of the peculiar features of this upper and lower molar series, with its strange collection of roots and alveoli, it is difficult to avoid conjecturing that, despite the simple crown-pattern of the anterior molar it is in reality very far from being a simple tooth. It is difficult to avoid speculating as to whether *Hydromys* has in reality simplified its dentition by the loss of a

molar. If the line of the palatal suture, or the origin of the posterior zygoma root, should prove to be at all stable points in cranial architecture, it would look as though the anterior lamina of the upper anterior molar occupied somewhat the same anatomical position as the whole of the anterior molar in more typical forms.

### RATTUS.

(1) *R. greyi*. Specimens from Mount Compass, South Australia. Identity established by Mr. Oldfield Thomas (Ann. & Mag. Nat. Hist. series 9, vol. viii. p. 425, October 1921).

### Upper Molars.

The crown-pattern of the upper molars is shown in text-fig. 6, A.

Text-figure 6.



Left upper molar series of *Rattus greyi*. A, showing the occlusal surface; and B, the alveolar cavities.

It is typical and needs no description.

The roots are small, their alveoli being a series of clean-cut



holes in the jaw-margin, and the tooth itself is not to any extent received in a depressed area of the jaw.

The anterior molar has 5 roots, a large single median anterior root and 4 others arranged in pairs behind it.

The second molar has 4 roots arranged as an anterior pair and a posterior pair. The third molar has an anterior pair of roots arranged labio-lingually and a single median posterior root. In the whole root series there is a single anterior median root, and a single posterior median root, and 5 lingual and 5 labial roots arranged in pairs (see text-fig. 6, B).

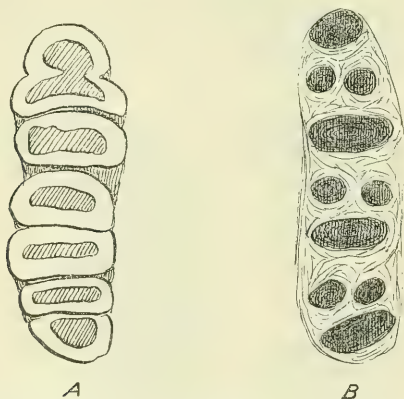
What might be termed the root-formula for the upper molars would therefore be 5. 4. 3.

#### *Lower Molars.*

The occlusal surface of the lower molars shows two sub-divisions of the crown of the two posterior molars and three sub-divisions of the anterior molar, the anterior and middle sub-divisions of the anterior tooth being often partially fused together (see text-fig. 7, A).

The root-cavities are well developed and clear cut, like those of the upper molars. The anterior tooth has 4 roots, consisting

Text-figure 7.



Left lower molar series of *Rattus greyi*. A, the occlusal surface; and B, the alveolar cavities.

of an anterior median rounded root followed by a pair of roots (lingual and labial), followed again by a single root elongated from side to side.

The second and third teeth have 3 roots each arranged as a pair of anterior rounded roots and a single elongated posterior root (see text-fig. 7, B). The lower root-formula could therefore be written as 4. 3. 3.

(2) *R. terre-regine* shows exactly the same condition as *R. greyi*

and the introduced forms *R. rattus* and *R. norvegicus* are identical. Evidently the unknown rat which lives on Goat Island is akin, as a comparison of text-figs. 1 & 7, B, will show.

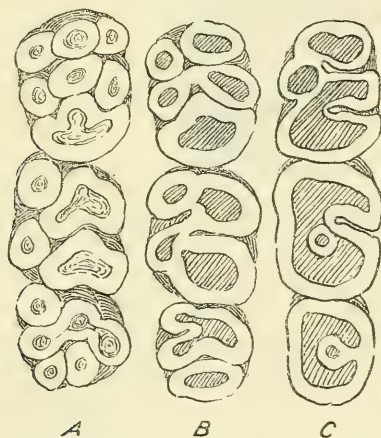
LEPORILLUS Oldfield Thomas, 1906.

The species examined is that recently named *L. jonesi* (Ann. & Mag. Nat. Hist. ser. 9, vol. viii. p. 618, Dec. 1921). All the examples come from Franklin Island in Nuyt's Archipelago, on which island the type was taken.

*Upper Molars.*

The upper molar occlusal pattern is shown at text-fig. 8. The molars are large and are deep set in the jaws. The alveolar cavities show a rather noteworthy sinking of the whole tooth into the alveolar area of the jaw; the cavities for the individual roots opening from an area which is itself somewhat below the general surface of the surrounding bone. (See text-fig. 9.)

Text-figure 8.



Left upper molar series of *Leporillus jonesi*. Three specimens, A, B, and C, showing the alteration of the occlusal pattern, with varying degrees of attrition.

The first molar has 3 roots, each having a distinct socket in the jaw. Of these three roots one is anterior and median, and the other two are posterior lingual and labial; the postero-lingual root in some specimens shows a tendency to be bifid.

The second molar also has 3 roots, but the lingual root is further advanced in the jaw so as to be more truly lingual, and not so postero-lingual in position.

The third molar has 2 roots, of which the anterior is elongated from side to side and shows a tendency to bifurcation; possibly

Text-figure 9.



Alveolar cavities of the left upper molar series of *Leporillus jonesi*.

it represents the anterior and lingual roots of the second molar. The root formula would therefore be 3. 3. 2.

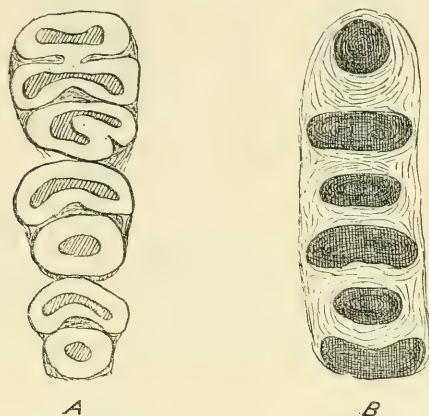
#### *Lower Molars.*

Of the lower molars the large anterior member shows three laminae on its occlusal surface, the second molar two laminae, and the third also two. The root-pattern shows the same reception of part of the crown into a depressed area of the jaw as is seen in the case of the upper teeth. (See text-fig. 10, B.) Each tooth is provided with 2 roots, and anterior rounded root, and a posterior one elongate from side to side. In the case of the first molar there is a tendency towards lateral bifurcation of the posterior root. The lower root-formula is therefore 2. 2. 2.

The rats whose remains have gone in such countless numbers to constitute the bone-deposits in the Buckalowie caves, had the molars sunk into the jaw in the same fashion as is seen in the Franklin Island *Leporillus*. They had the same root-formula above and below (see text-fig. 2 and compare text-figs. 9 & 10);

they also seem to have had the same crown pattern, certainly they had not the crown pattern which is distinctive of *Conilurus*. The measurements of fragments of their skulls are practically those of the Franklin Island *Leporillus*; and it is probably not far from the truth to say that a rat very like the modern insular

Text-figure 10.



Left lower molar series of *Leporillus jonesi*. A. Occlusal surface.  
B. Alveolar cavities.

form was a contemporary of *Thylacoleo* and *Thylacinus* in the northern parts of South Australia. No traces of living rats were seen at Buckalowie, nor do the guano-miners know of the presence of any in the district.

#### NOROMYS Lesson, 1842.

The only example of this genus that I have been able to examine is *N. cervinus*, the specimen coming from Miller's Creek to the west of Lake Eyre.

The specimen is one which shows very little wearing of the occlusal surfaces of the molars. There is seen the same tendency for the tooth to be received in a depression of the jaw as was noted in *Leporillus*. The root-pattern is also reminiscent of that genus, for the upper molars 1 and 2 are 3-rooted teeth, the roots being one anterior and two posterior. The third molar, however (in the only specimen examined), showed a single cavity which contained a partially subdivided root. (See text-figure 11.)

The root-formula would therefore be 3. 3. 1.

The lower molars are all 2-rooted teeth, but there is a well-marked tendency towards reduction of the posterior root of the third molar. The root-formula is 2. 2. 2.

Text-figure 11.



Left upper molar series of *Notomys cervinus*. A. Occlusal surface.  
B. Alveolar cavities.

Text-figure 12.

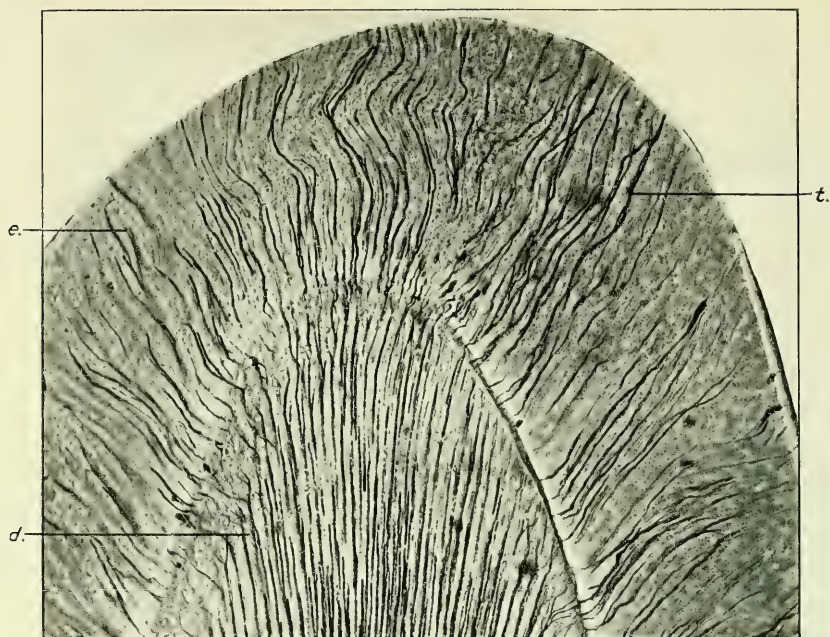


Lower molar series of *Notomys cervinus*. A. Left upper molar crown-pattern.  
B. Right lower molar root cavities.

CONCLUSION.—It is suggested that the study of the molar root-pattern, and the expression of what might be termed a root-formula, are of some importance in systematic work among the Murines. Unfortunately it is not possible in Adelaide to carry out even a partial survey of the Australian rodents, for the material is not obtainable, but it is hoped that such workers as possess material will record the root-patterns of *Conilurus*, *Mastacomys*, and other interesting Australian forms.







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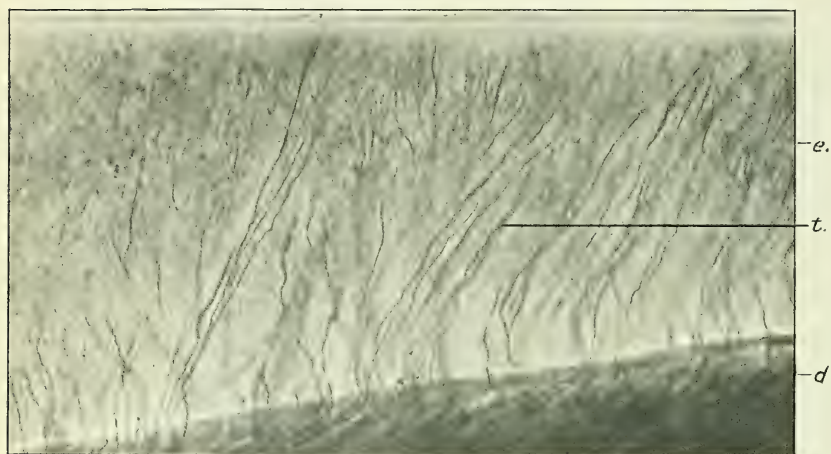
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STRUCTURE OF THE ENAMEL IN THE PRIMATES.

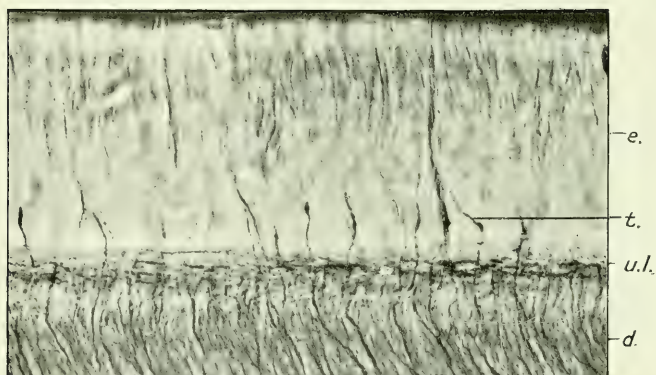




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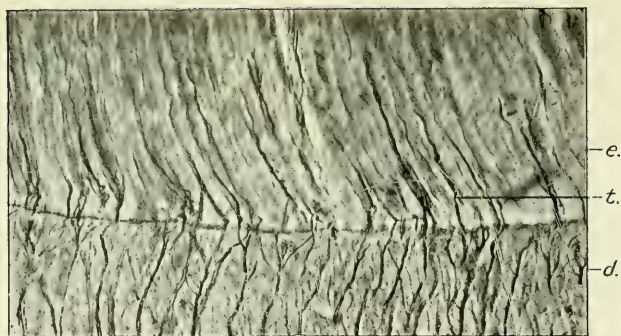
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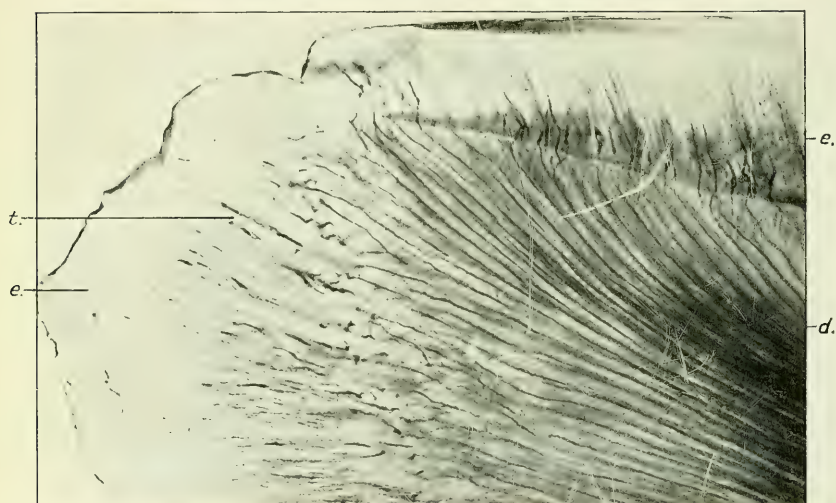
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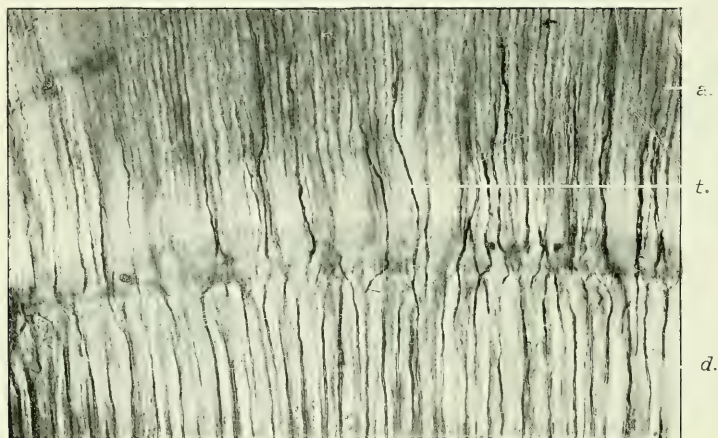




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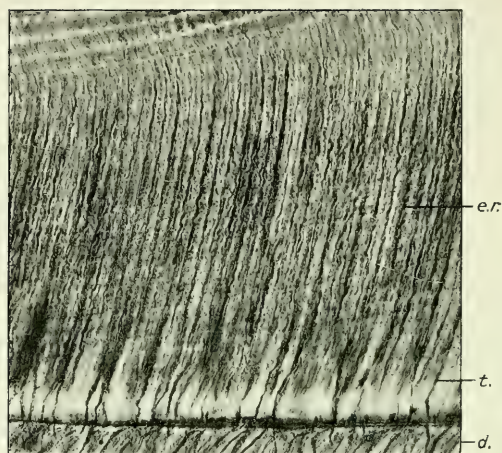


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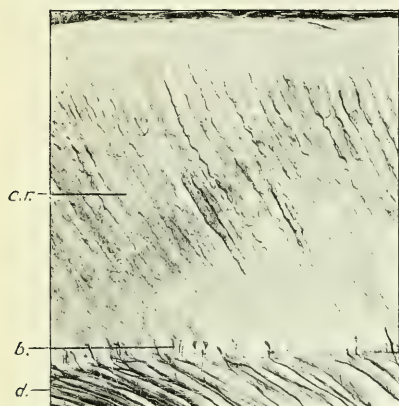


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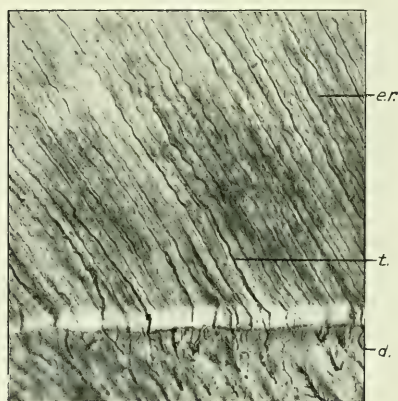




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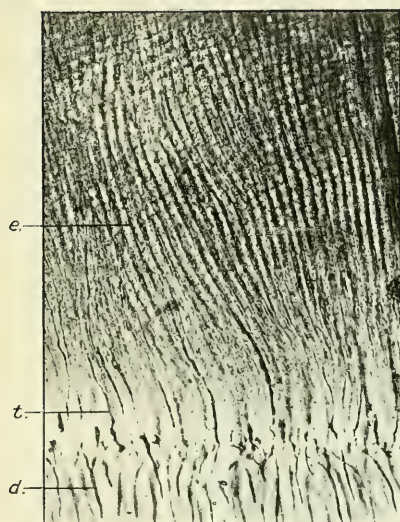


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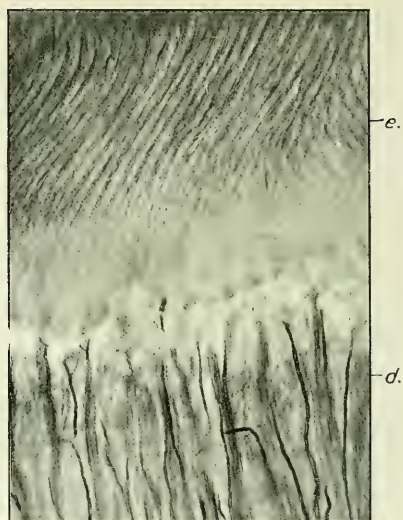
STRUCTURE OF THE ENAMEL IN THE PRIMATES.



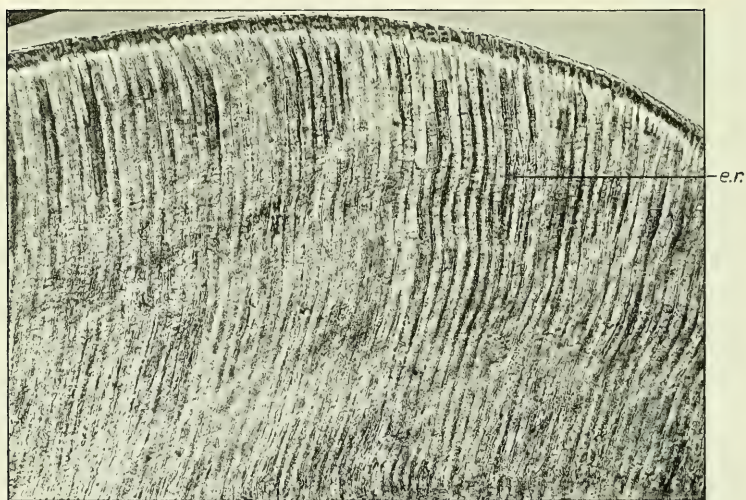




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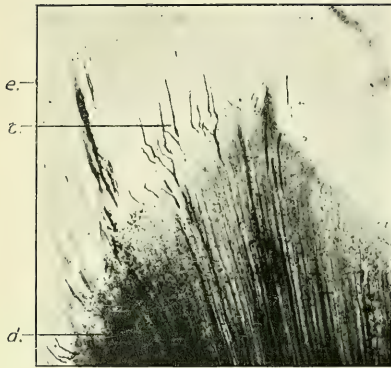
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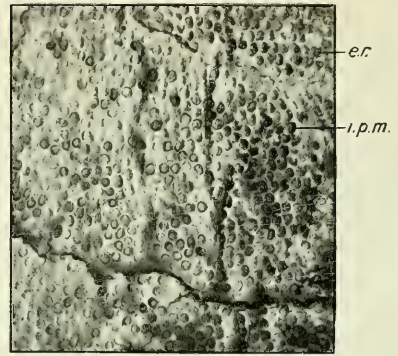
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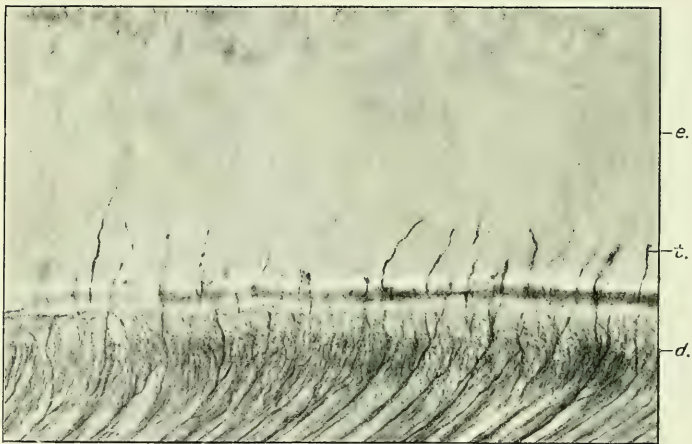




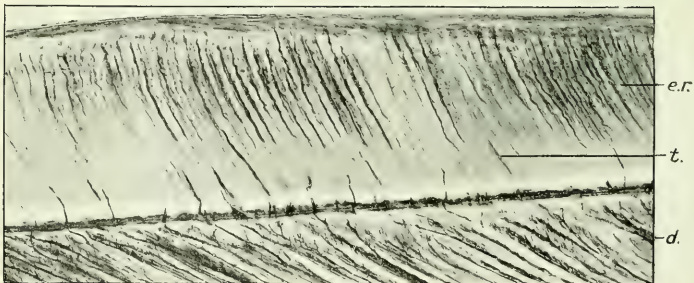
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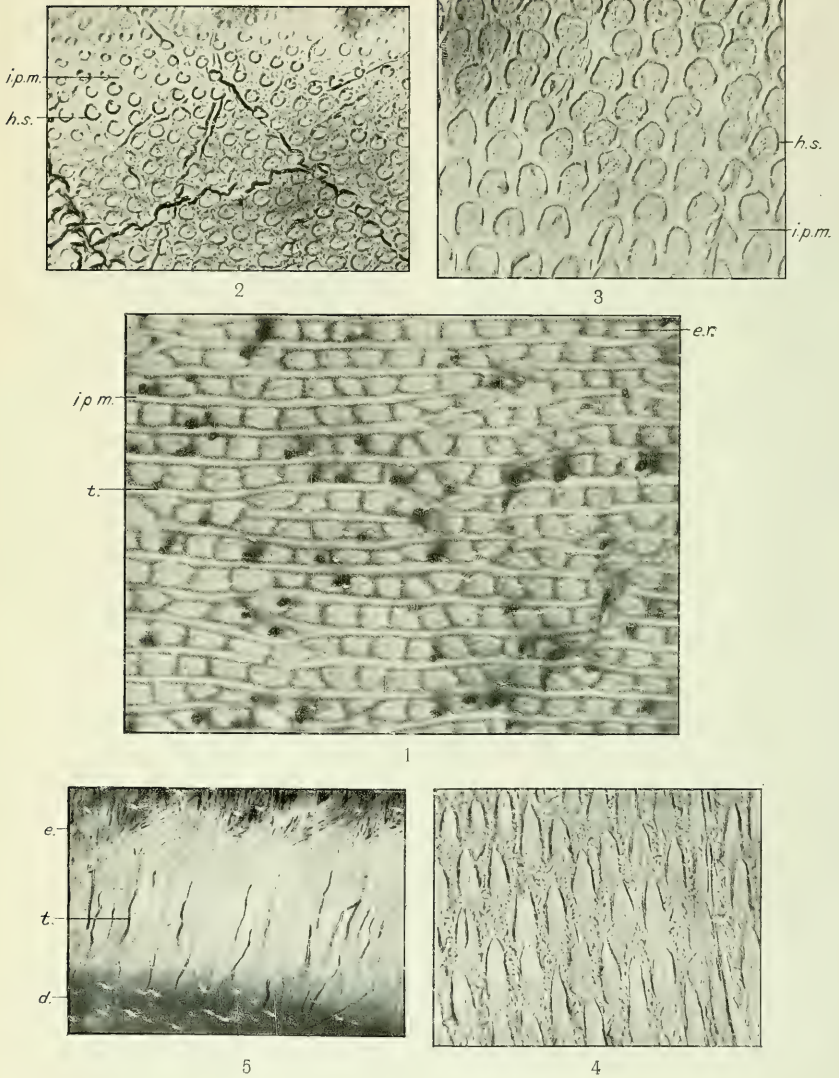


3



4





STRUCTURE OF THE ENAMEL IN THE PRIMATES.

30. On the Structure of the Enamel in the Primates and some other Mammals. By J. THORNTON CARTER, Hon. Research Assistant, University College, University of London.

[Received May 24, 1922: Read June 13, 1922.]

(Plates I. to VII. \*)

During the past forty years the theory of the evolution of the crowns of mammalian molar teeth, which is associated with the names of Cope and of Osborn, has attracted the attention of a large number of workers, so that a voluminous literature on the subject has accumulated.

Whilst so much work has been devoted to the gross forms of the teeth, it is surprising to find that little attention has been given to the minute anatomy of the dental tissues as evidence in throwing light on the problem of affinity.

In the year 1850, Sir John Tomes, F.R.S., submitted to the Royal Society a contribution, entitled "The Structure of the Dental Tissues of the Order Rodentia" (Phil. Trans. 1850), in which he gave a detailed description of the pattern of the enamel in various genera, and from their comparison drew the interesting conclusion that the various families of Rodents possess a "constant and exclusive character in the structure of the enamel"; further, that there is a "different and distinct character in each of the larger groups, and that the variety of structure is constant throughout members of the same group: we may take, for example, the Scuridæ, the Muridæ, and the Hystrioidæ, in each of which the structure of the enamel is different and in each is highly distinctive" . . . . . "the varieties in the structure of the dental tissue, with a few isolated exceptions, justify and accord with the arrangements of the order into the several divisions proposed by Mr. Waterhouse and deduced by him from the relations of the several parts of the skull."

Yet a year earlier than the publication of his observations on the histology of the enamel in Rodents, Tomes had contributed to the Philosophical Transactions a paper "On the Dental Tissues in Marsupial Animals" (Phil. Trans. 1849, vol. cxxxix.), in which he demonstrated a marked feature in their enamel in the form of a system of tubes continuous with the dentinal tubes, this being a constant character of the teeth of all Marsupials, excepting only those of the Wombat. This character "attains its utmost development in the Macropodidæ, and is more feebly present in some Dasyuridæ, whilst in *Myrmecobius* and yet further in

\* For explanation of the Plates, see p. 607.



*Tarsipes* it is reduced to small limits" (Tomes, Dental Anatomy, p. 43).

The significance and value of these contributions lies in the fact that Tomes demonstrated clearly that the enamel pattern in Rodents provides a specific criterion of affinity, and that the structure of the enamel in Marsupials, taken in conjunction with other anatomical characters, may be employed to demonstrate Marsupial relationship.

Seventy years have passed since the publication of these researches, but, in so far as I am aware, during that period no one has extended Tomes's work and published the results of the examination of the enamel structure in all the representative members of a diversified order; and further, with the exception of Sir Charles Tomes, F.R.S., the distinguished son of a distinguished father, no one has applied the results obtained to the determination of affinities or relationship in the case of extinct mammals. In a paper on the "Minute Structure of the Teeth of Creodonts, with special reference to their suggested resemblance to Marsupials" (P. Z. S. 1906), Sir C. Tomes employed the character of tubular enamel as a test of Marsupial relationship, and found that in none of the Creodont teeth which he examined was this character present. Included with this Creodont material was a portion of a tooth of *Borhyaena*, one of the Sparassodonta, in the enamel of which Tomes found no trace of tubes. But the Marsupial characters of this group were so numerous that Prof. D. M. S. Watson, F.R.S., asked me to undertake a further examination of the enamel in other members of the suborder, and I was fortunate enough to discover this Marsupial character in the teeth of *Cladosictis*, *Pharsophorus*, and of *Borhyaena* (Journ. Anat. 1919).

Following the provision of the material for the examination of Sparassodont teeth, the authorities of the American Museum of Natural History handed over to me a rich and representative collection of teeth and jaws of Eocene mammals, comprising some eighty genera, which had been formed for the purpose of obtaining a set of sections with the hope that, in the words of Dr. Matthew, "the investigation thereof will provide a new line of evidence for the affinities of mammals, as distinct from the skeleton or the teeth or the soft anatomy" . . . . and to "have a cross check on relations of the same kind as the cross check between teeth adaptations and feet adaptations." Already several hundreds of sections have been prepared from this material, and the results obtained encourage the hope that Dr. Matthew's expectations will be fulfilled. To obtain the utmost value from such a collection, it is desirable to possess a complete series of sections of teeth of every genus of existing mammalia, and, in consequence, I have laboured to build up a collection of ground sections which should embrace not only representatives of each genus, but also, in so far as is possible, sections of each tooth in the individual dentition.

Included in the material supplied by the American Museum are teeth of Eocene Primates and Menotyphla: this material was found to be highly fossilized and very friable, and before examining it thoroughly, I decided to complete my collection of tooth sections of recent Primates. A large number of old-world and new-world monkeys have been examined, and some 200 sections have been prepared from teeth of practically all the members of the suborder Lemuroidea.

The results obtained from this microscopical examination disclose certain new features, which, taken in conjunction with other anatomical characters, should be of value.

The first striking feature to be recorded is that throughout the whole suborder Lemuroidea a constant feature in the enamel is a regular system of tubes continuous with the dentinal tubes. *Chiromys* provides a solitary exception, and thus occupies a position similar to *Phascolomys* amongst the Marsupials. The richness of penetration varies greatly both in the teeth of different families and also in different areas of the enamel of individual teeth\*.

In the Lemuriformes the amount of penetration is usually slight, seldom exceeding the extent shown in Pl. II. fig. 2, where the tubes (*t*) are seen to pass through about half the thickness of the enamel: over the apex of the unworn incisor teeth and in the cusps of the molars the tubes often pass outwards to within a short distance of the free surface, as shown in Pl. III. fig. 2. As one passes downwards towards the neck of the tooth and the enamel becomes thinner, the penetration becomes more sparse, most of the dentinal tubes splitting up into a fine brushwork just beneath the enamel surface. Such tubes as pass over into the enamel traverse a layer of uncalcified tissue shown in Pl. II. figs. 1 & 2 and designated by the letters *u.l*.

In the Indrisinæ the tubular penetration is extremely rich, rivalling the extent found in the Macropodidæ; for over the apices of the cusps of all the teeth there are tubes in the enamel continuous with almost every dentinal tube, and these pass outwards through the greater thickness of the enamel. The illustrations shown in Pl. I. figs. 1 & 2 give a clearer idea of this condition than can be conveyed by a verbal description.

Towards the necks of the teeth the penetration is still quite rich, but in the sulcuses of the crowns of the molars the penetration does not proceed to any great extent.

In *Propithecus* the degree of penetration is markedly less than in the Indrisinæ, but in certain areas of the enamel it is a conspicuous feature (Pl. II. fig. 3).

In the Lorisinæ there is a very rich penetration, attaining its

\* For simplicity I retain the terms "tube" and "penetration," since they are employed in all text-books in the description of this condition in the enamel, but I consider the so-called tubes to be fibrils, epiblastic in origin, and though continuous with the dentinal fibrils, they are not a penetration of these structures into the enamel (*vide* Carter, Phil. Trans. Roy. Soc. ser. B, cccviii. 1917).

greatest development in the enamel of the tooth-cusps. With a view to economy of illustration, I have not included a photo-micrograph of their enamel, resembling as it does the enamel of the Galagos, illustrated in Pl. III. fig. 3.

In *Perodicticus potto* (Pl. VI. fig. 4) the penetration is not nearly so rich as in the Lorises and the Galagos, whilst in *Nycticebus* (Pl. VI. fig. 3) it is but slight, many of the tubes in the enamel of the molars ending just within the enamel in the form of small bulbous spindles similar to those shown in the enamel of *Callithrix* (Pl. IV. fig. 3).

In *Tarsius*, concerning whose position in the classification of the Primates so much has been written in recent years, the penetration attains a degree of richness even greater than is found in the enamel of *Galago*, and rivals in extent the condition shown in *Indris* (Pl. III. fig. 1).

The actual structure of the enamel in the Lemurs also presents features of great interest, inasmuch as one finds that in sections of the entire tooth, the general pattern, or form and arrangement of the prisms, in the Asian and African forms differs from that of the Mascarene Lemurs, and that the enamel of *Tarsius* is to all intents and purposes identical with that of *Galago*.

The pattern of the Mascarene genera is shown in the photo-micrograph of a molar of *Indris* (Pl. V. fig. 1), and this pattern is constant for all the genera, including *Chiromys* (Pl. V. fig. 2). Immediately beneath, on the same plate, is a photo-micrograph of a portion of the enamel of *Semnopithecus* (Pl. V. fig. 3), and it will be seen that the general structure is closely similar to the two lemurs, the enamel being composed of prisms or rods of a somewhat granular structure and with straight, even margins, the prisms being separated one from another by a slight amount of calcified interstitial substance.

The enamel pattern in the Asian and African Lemurs is quite distinct from that seen in the Mascarene forms. It is composed of rods or prisms with undulating margins, which in longitudinal section present a sharply-defined picture showing the wavy outline of the margins of the rods (Pl. IV. fig. 1). In transverse section (Pl. VI. fig. 2) these are seen to be cylindrical rods (*e.r.*), separated one from another by a considerable amount of the calcified interstitial substance usually designated by workers on the histology of enamel as the interprismatic material (*i.p.m.*).

A pattern of enamel identical with this obtains in the teeth of the Hapalidæ and the Cebidæ. In *Callithrix*, which Gregory regards as a very primitive form, there is a slight degree of penetration of the enamel, the prolongation of the dentinal tubes terminating in the enamel (*e*) in the form of little bulbous spindles (*b*) (Pl. IV. fig. 3). The close similarity of the enamel pattern of *Callithrix*, which is identical with that of all other Platyrrhines, to the pattern of *Galago* and of *Tarsius* will be apparent on comparing the micro-photographs figured (Pl. IV.).

I have prepared sections of teeth of *Megaladapis grandidieri* and of *Palaeopropithecus* from the Pleistocene of Madagascar. In the former penetration was almost absent, but in *Palaeopropithecus* a system of tube is present, developed to an extent which equals the condition seen in the teeth of *Propithecus* itself (Pl. II. fig. 3).

In pattern both forms have an enamel identical with that of the recent Mascarene forms.

The microscopic examination of the enamel in Primates therefore discloses certain features which have not been noted before. They are:—

(1) The enamel in all Lemurs, with the exception of *Chiromys*, possesses a system of tubes continuous with the dentinal tubes. In *Indris* and *Propithecus* the penetration is very rich, but in the Lemurinae it is feebly developed. In the Galagos, the Lorises, and in *Perodicticus potto* the penetration is rich also, but in *Nycticebus* it is slight, so slight, in fact, that except in the apices of the cusps, the penetration is reduced to a degree which is but little greater than one finds in the teeth of the South American monkeys.

(2) There is a marked and constant difference between the enamel pattern in the Mascarene forms and the Asian and African forms, the enamel in the former having a pattern identical with that found in the Catarrhines, whilst the Asian and African forms present a pattern identical with that seen in the teeth of the Platyrrhines. The Lemuroidea, therefore, parallel the Anthroipoidea in enamel structure.

(3) *Tarsius* has an enamel indistinguishable in sections from that of *Galago*.

Amongst living mammals the penetration of the enamel by tubes is, as already stated, a character found in all Marsupials, *Phascolomys* excepted. No other order possesses this character as a constant feature of all its genera.

In the order Insectivora, however, there are a number of genera which do possess it. In the Menotyphla one finds an extremely rich penetration in the enamel of the Macroscelidæ (*Petrodromus* and *Rhyncocyon* were examined), but in sections prepared from a large number of teeth from skulls of *Tupaia* there is no trace of any penetration. In the Lipotyphla all teeth of Soricinæ and of Crocidurinae have enamel which is richly tubular. *Erinaceus* has a moderate degree of penetration, but *Gymnura* has none. The Talpinae also do not disclose any penetration.

The two genera comprising the suborder Hyracoidea have an enamel which is richly tubular.

The only other living mammal which possesses this character in the enamel is the Jerboa, one solitary creature out of the large number comprising the order Rodentia.

In the enamel of the teeth of all fossil Marsupials which I have



examined, extending back to *Peradectes* (from the Tiffany beds of Colorado (Lower Eocene)), there is a penetration.

In the suborder Multituberculata (Allotheria), which Dr. Matthew tells me he regards as in the Metatherian stage of evolution, but separate from the Marsupials and Placentals, I have also discovered a rich penetration and a distinct pattern of enamel, which will be alluded to later in this communication.

With the presentation of fresh details of the minute anatomy of the teeth the first question to arise is that of their significance.

Is the tubular system of the enamel to be regarded as an heritage derived from remoter ancestors, or has it some adaptive significance in relation to the present needs of its possessor?

To throw light on the question, I have prepared sections of teeth of several primitive Primates.

In the enamel of *Notharctus* and of *Pelycodus*, undoubted Lemuroid Primates from the Lower Eocene, I have been able to discover no trace of penetration by tubes, although I have prepared a number of sections from teeth of different specimens.

In *Hemiacodon*, one of the Anaptomorphidæ from the Middle Eocene, there is marked penetration, well shown in Pl. VI. fig. 1, where, in the enamel over the apex of the tooth, the tubes (*t*) are clearly shown passing some distance into the enamel, though a little further down in the crown of the same tooth all trace of structure, in both enamel and in dentine, had become obliterated in the process of fossilization.

In *Phenacolemur*, concerning whose affinities there has been some discussion (Broili and Schlosser including it amongst the Insectivores, whilst Dr. Matthew, in his list of Eocene material supplied to me, includes it amongst the Menotyphla), the enamel is also tubular.

*Nothodectes* (*Plesiadapis*), whose affinities also are doubtful, discloses no sign of penetration, and the structure of its enamel lends no support to the views of Stehlin that it is closely akin to the Chiromyidæ, but rather supports the opinion of Matthew that it is nearer to the Menotyphla, and is a primitive synthetic type intermediate between Tupaiaoids and Lemuroids.

With regard to the microstructure of the enamel in these extinct Primates, it is interesting to record that *Hemiacodon* possessed an enamel identical in pattern with that of *Tarsius* of the Asian and African Lemurs, and therefore with that of the Platyrrhinæ, whilst *Notharctus* and its forerunners *Pelycodus* disclose a structure similar to that found in the Mascarene forms, living and extinct, and to the Catarrhinæ.

It is obvious, therefore, that, in the examination of a fragment of a tooth, the discovery of the presence of a system of tubes in the enamel, unsupported by other evidence, would not afford a precise test of affinity; but, taken in conjunction with the pattern of the enamel, the demonstration of tubes would enable one to state, with a degree of certainty, as to whether such a fragment



had been derived from a Multituberculate, a Marsupial, an Insectivore, a Lemur, or whether the tooth was that of a Jerboa; and further, as the evidence adduced in this paper shows, in the case of a Lemur one could differentiate between the Mascarene and the Asian and African forms.

It remains for me to give a very brief description in general of the tubular enamels of those mammals apart from the Lemurs to which I have alluded.

The enamel pattern of the Multituberculates is quite distinctive, and differs fundamentally from all others which I have examined. If a section of a tooth of *Polymastodon* be ground and examined (Pl. VII. fig. 5), tubes (*t*) will be seen passing from the dentine (*d*) into the enamel (*e*): by careful illumination a faint pattern may be discerned, which can be developed by washing the section for a time in acid alcohol until such an image as is shown in Pl. VII. figs. 2, 3, and 4 is disclosed.

Here one sees a series of horseshoe-shaped bodies (*h.s.*), which become smaller and more widely separated as the outer edge of the enamel is approached. In whatever plane the section may be cut these structures never become complete circles, the two ends remaining apart and terminating in bulbous slightly recurved enlargements. Such an image would be seen in transverse section of any spiral structure.

Any further description of the minute structure of this peculiar enamel would be out of place in this paper, but it may be mentioned that *Ptilodus* also has an enamel which is richly tubular and an enamel pattern similar to, but by no means identical with, that of *Polymastodon*.

The Marsupials possess a very distinctive general pattern, as is shown in Pl. VII. fig. 1, where the rods or prisms (*p*) are seen, in transverse section, to be arranged in rows which sometimes merge: these rows are separated by a very definite area of interprismatic material (*i.p.m.*), so that, as Dr. Mummery has pointed out, in teased preparations of developing enamel this substance splits up into laminae. The dark dots (*t*) are the so-called tubes seen in section. A section showing the enamel prisms in such rows and presenting the tube-penetration is peculiar to Marsupials.

I have not figured the richly tubular enamel of the Jerboa, but it is the only rodent which shows any trace of tube-penetration, and its enamel pattern presents the criss-cross arrangement of the rods which Sir John Tomes showed to be a character peculiar to the Rodents.

With regard to the significance of the presence of a system of tubes in the enamel, the variability of its degree and of its distribution and the fact that, whilst richly developed in one creature it may be totally absent in a closely-related form, would seem to indicate that it is connected with some adaptive process, and that, taken alone, it has little or no value as evidence of affinity or line of descent.

The microstructure of the enamel, however, appears to be particularly constant. In the long and well-authenticated series of creatures comprising the ancestry of the Horses, the microstructure of the enamel does not change, in spite of the modification of the teeth from the brachydont form in *Eohippus* through all the progressive stages leading up to the complex hypsodont molar teeth of recent horses.

In the Marsupials the pattern of the enamel in recent and fossil Australian forms appears to be identical with that of the teeth of *Peradectes* from the Tiffany beds of Colorado (Lower Eocene).

Certain fossil rodents from the Eocene exhibit a close similarity in enamel structure to recent forms, and where, as in *Chiromys*, a Lemur has evolved a rodent dentition, the structure of its enamel still retains its Lemurine character.

It was my intention to hold over a description of the minute structure of the teeth of Primates until I had published an account of the structure of the teeth in Insectivores, recent and fossil, and of the primitive Creodonts, the material for which has been examined, together with that of a large number of other Eocene mammals. But Professor J. P. Hill, F.R.S., and Professor D. M. S. Watson, F.R.S., were of the opinion that the facts presented in this communication would be of immediate interest to the Fellows of the Society, the more so as recent palæontological discoveries have provided fresh evidence of the antiquity of the Higher Primates.

In conclusion, I have to express my deep gratitude to my colleague, Major G. S. Sansom, and to Mr. F. J. Pittock for their kindness in preparing the micro-photographs used in the illustrations, and to Professors Hill and Watson for constant encouragement.

Above all I have to thank Dr. W. D. Matthew, F.R.S., for providing invaluable material, and for most valuable information and suggestion in conversation during his recent visit to Europe.

Most of the recent material employed was acquired by purchase, but I am deeply indebted to the Zoological Society through Mr. R. I. Pocock, F.R.S., for the gift of teeth of *Chiromys*, and to Professor J. Elliot Smith, F.R.S., for a mandible of *Tarsius*.

#### *Summary.*

A microscopical examination of the teeth of Primates discloses the fact that all members of the suborder Lemuroidea possess, in a varying extent, the character of a penetration of tubes into the enamel.

In the Lemurinae this penetration is slight, but in the Indrisinae it is very rich.

The Galagos and Pottos also have a rich penetration, but in *Nycticebus* it is but feeble.

*Tarsius* has an enamel richly tubular, and in its structure essentially Lemurine.

A further interesting feature is that the pattern of the enamel in the Mascarene Lemurs differs from that of the Asian and African forms, and that the former has a structure identical with that found in the enamel of all Catarrhines, whilst the structure of the enamel in the Platyrrhines is identical with that found in the Asian and African Lemurs.

Two primitive Lemuroid Primates, *Pelycodus* and *Notharctus*, from the Eocene show no penetration, but in the structure of their enamel resemble the Mascarene Lemurs.

*Hemiaodon*, a Tarsioid Primate, also from the Eocene, has an enamel which is tubular, and in structure appears identical with the enamel of the recent *Tarsius*.

The enamel pattern affords a useful test of affinity if taken in conjunction with the character of a tube-penetration, and enables one to discriminate between Multituberculates, Marsupials, and Placentals.

#### EXPLANATION OF THE PLATES.

The following is a list of reference letters common to the various figures:—

<i>b.</i> bulbous spindles.		<i>h.s.</i> horseshoe-shaped bodies.
<i>d.</i> dentine.		<i>i.p.m.</i> interprismatic material.
<i>e.</i> enamel.		<i>u.l.</i> uncalcified layer.
<i>e.r.</i> enamel rods.		

#### PLATE I.

- Fig. 1. Longitudinal section through the incisor of *Indris*, showing the presence in the enamel (*e*) of tubes (*t*) continuous with those of the dentine.  $\times 180$   
 Fig. 2. Longitudinal section through the protocone of an upper molar of *Indris*, showing a similar condition to that seen in fig. 1.  $\times 180$ .

#### PLATE II.

- Fig. 1. Longitudinal section of a lower incisor of *Lemur catta*, showing the form and structure of the enamel rods or prisms (*p*), and at the surface of the dentine (*d*) next the enamel a layer of uncalcified material (*u.l.*).  $\times 350$ .  
 Fig. 2. Longitudinal section of a lower incisor of *Lemur*, showing the passage of tubes (*t*) from the dentine (*d*) into the enamel (*e*); the tubes traversing the layer of uncalcified material (*u.l.*) are shown in fig. 1.  $\times 350$ .  
 Fig. 3. Section of a lower premolar of *Propithecus*, showing the presence of tubes (*t*) in the enamel (*e*).  $\times 300$ .

#### PLATE III.

- Fig. 1. Section of a tooth of *Tarsius*, showing the junction of the tubes (*t*) in the enamel (*e*) with those of the dentine (*d*).  $\times 450$ .  
 Fig. 2. Section of a lower incisor of *Microcebus*.  $\times 250$ .  
 Fig. 3. Section from the coronal surface of a lower molar of *Galago*.  $\times 350$ .

#### PLATE IV.

- Fig. 1. Section of a tooth of *Tarsius*, showing the general pattern of the enamel (*e*) with the undulating margins of the enamel rods (*e.r.*) and the tubes (*t*) in the enamel.  $\times 350$ .  
 Fig. 2. Section of a tooth of *Galago*, presenting an appearance identical with that shown in fig. 1.  $\times 340$ .  
 Fig. 3. Section of a premolar tooth of *Callithrix* (*Callicebus*), showing an enamel pattern similar to *Tarsius* and to *Galago*. The dentinal tubes terminate a very short distance within the enamel as little bulbous spindles (*b*).  $\times 350$ .

## PLATE V.

- Fig. 1. Section of the occlusal surface of the left upper molar of *Indris*; the photomicrograph taken from the same tooth as the illustration shown in Pl. I. fig. 2. The tubes (*t*) pass but a short distance into the enamel (*e*). The pattern of the enamel is clearly shown, the enamel rods (*e.r.*) having straight margins and showing a fine granular structure.  $\times 450$ .
- Fig. 2. Section of a molar of *Chiromys*. The dentinal tubes terminate at the amelodentinal junction. The pattern of the enamel is similar to that of the other Mascarene Lemurs.  $\times 500$ .
- Fig. 3. Section of enamel of *Semnopithecus*.  $\times 450$ .

## PLATE VI.

- Fig. 1. Section of a cusp of a molar of *Hemiacodon*, showing the presence of tubes (*t*) in the enamel (*e*).  $\times 275$ .
- Fig. 2. Transverse section of an incisor of *Galago*, showing the enamel rods (*e.r.*) cut across and having a circular form separated one from another by a considerable amount of interprismatic material (*i.p.m.*).  $\times 300$ .
- Fig. 3. Section of a molar of *Nycticebus*, showing the slight amount of penetration of the "tubes" (*t*) into the enamel, whilst many end in a bulbous spindle (*b*) similar to those shown in the enamel of *Callithrix* (Pl. IV. fig. 3).  $\times 300$ .
- Fig. 4. Section of an incisor of *Perodicticus potto*, showing the passage of tubes (*t*) and an enamel pattern identical with that seen in *Galago* and in *Tarsius*.  $\times 340$ .

## PLATE VII.

- Fig. 1. Section of an incisor of *Macropus ruficollis*, showing the enamel rods (*e.r.*), cut transversely, lying in rows which are separated by sharply-defined areas of interprismatic material (*i.p.m.*). The "tubes" of the enamel are seen as black dots (*t*).  $\times 1500$ .
- Fig. 2. A transverse section of the enamel of a molar of *Polymastodon*, etched to show the structure. The horseshoe-shaped bodies with bulbous ends (*h.s.*) would suggest sections through an elongated spiral since they never form complete rings.  $\times 275$ .
- Fig. 3. Transverse section through the enamel of the lower incisor of *Polymastodon*, showing a similar condition to that seen in fig. 2, but demonstrating a finely granular structure of the areas embraced within the horseshoe-shaped bodies.  $\times 400$ .
- Fig. 4. Longitudinal section of the enamel of a molar.  $\times 480$ .
- Fig. 5. Unetched section of a molar of *Polymastodon*, showing the passage of tubes (*t*) from the dentine (*d*) into the enamel (*e*).  $\times 300$ .







1



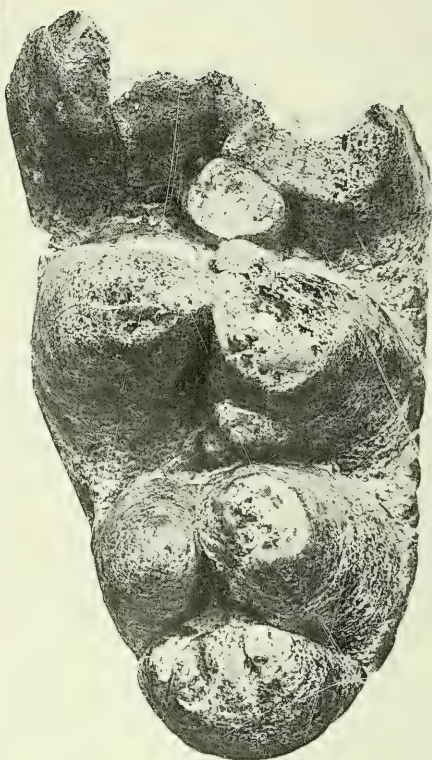
2

*PROBOSCIDIA* from BALUCHISTAN.





1



2

*PROBOSCIDA* from BALUCHISTAN.





1

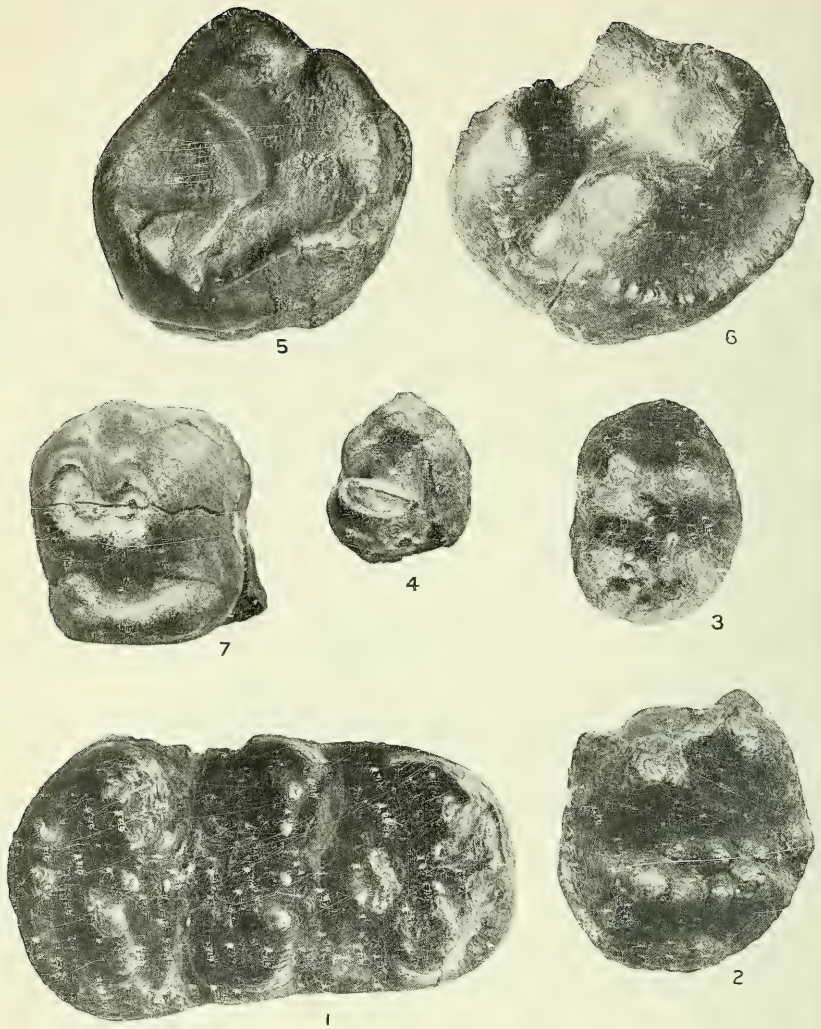


2

*PROBOSCIDA* from BALUCHISTAN.







*PROBOSCIDIA* from BALUCHISTAN.

31. Miocene Proboscida from Baluchistan. By C. FORSTER  
COOPER, M.A., F.Z.S., Superintendent of the University  
Museum of Zoology, Cambridge.

[Received May 3, 1922 : Read May 23, 1922.]

(Plates I.-IV.\* and Text-figures 1-12.)

The present paper contains a description of some Proboscidian remains obtained during two expeditions to the Lower Miocene deposits of Dera Bugti in Baluchistan.

These fragments are of interest, as they throw some further light on the earliest known Indian Elephants which have been described partly as a variety of *Bunolophodon angustidens* † and partly as belonging to a genus, *Hemimastodon* ‡, not known elsewhere. There are also teeth and a fragment of a lower jaw of a small *Dinotherium*.

Schlesinger §, in his beautifully illustrated account of the Mastodons in the Natural History Museum of Vienna, has figured and described two forms of *B. angustidens*. The criteria for distinguishing these two varieties lie, according to him, in the structure of the molars, and his description seems to refer especially to the intermediate teeth as being the more commonly found remains. In both forms the ridges consist of a large round outer cusp on the outer side of the tooth, with a smaller cusp pressed against its inner border and with one or more additional cusps in the valleys which separate the ridges. On the inner side of the tooth the ridge is continued by two similar main cusps—a larger on the outer side of the tooth and a smaller on the median side, but without any accessory cusps in the valleys.

Of the two varieties, one, which Schlesinger calls var. *typica*, shows these cusps as round in section and rather separate from one another, the surface of wear of the cusps being circular and flat with the general surface of the tooth; the other, var. *sub-tapiroidea*, differs in having the cusps more elliptical in section and less separate from one another, the accessory columns are less developed, and the areas of wear are oval and their planes slope from the general level of the tooth. While making these distinctions, Schlesinger at the same time denies the validity of

\* For explanation of the Plates, see page 626.

† Lydekker, 'Palæontologia Indica,' ser. 10, vol. vii. pt. 4, pp. 23-25 (1884). I use this generic name after Schlesinger, with whose work the chief comparisons in this paper are made and without prejudice to other names. The British Museum uses the name *Tetrabelodon*. My friend Professor H. F. Osborn writes to me since this paper was set up in type that he prefers the name *Trilophodon*.

‡ Pilgrim, 'Palæontologia Indica,' n. s. vol. iv. pt. 2, p. 17 (1912).

§ Schlesinger, Mitt. Geol. Geselt. Wien, Bd. xi. p. 133 (1918).

Lydekker's variety *palæindica*, which was founded chiefly on a third lower molar and which he states is within the range of variation of var. *typica*. The specimens now to be described tend, if anything, to reverse Schlesinger's view and in part to confirm Lydekker's.

The material in the collection consists of two palates of *B. angustidens* of slightly different age, part of a lower jaw belonging to the older of the two palates, and some separate upper and lower molar and premolar teeth.

The younger of the two palates (text-fig. 1) has on each side the last premolar and first molar in moderate wear, and the second molar erupting and unused. In front are the broken roots of the third premolar. Beyond this point and behind the second molars the specimen ends. The fourth premolars are weathered, but show a square outline and four subequal cusps a little elongated in the transverse direction. There is a shelf in front and low talon behind, and there are no intermediate cusps. They are very similar in size and shape to a corresponding tooth figured by Schlesinger for *B. longirostre*. There is no sign of a successional tooth underneath, so that it is not likely that they are imperfect milk teeth.

The first molars are three-ridged, with a very small talon. The first two ridges are worn, the third as yet untouched. They agree more with those figured by Schlesinger as var. *subtapiroidea*\* than as var. *typica*†.

The second molars, again, agree best with the figures of *subtapiroidea*‡, but here the cusps seem more separate from each other, a difference which may be more apparent than real, and due in large measure to the tooth being unworn; an internal accessory cusp on the third ridge is more prominent than his figures show.

The other palate is rather older in that the second molar is now in wear on the first two ridges. The specimen on its right side has an open socket, from which the third premolar has fallen out; the fourth premolar and first molar are well worn, the second is partly in wear, and the front ridge of the third is preserved in the alveolus. It is clear that this animal had two premolars and two molars in simultaneous wear, which is a longer time than Andrews§ suggests for this species. The present specimen appears to show that these four teeth remain until the third molar erupts, when it finally pushes the premolars and first molar forward and out. This is consonant with the view, supported by other reasons, that the stage of *angustidens* represented by these Indian forms is earlier than that of the more typical French forms from Sansan etc., and is possibly as early as any yet described.

The structure of the teeth in this second palate is essentially the same as in the other, except that in the second molars the

\* Schlesinger, Mitt. Geol. Geselt. Wien, Bd. xi. pl. iii. fig. 2.

† Loc. cit. pl. ii. fig. 2.

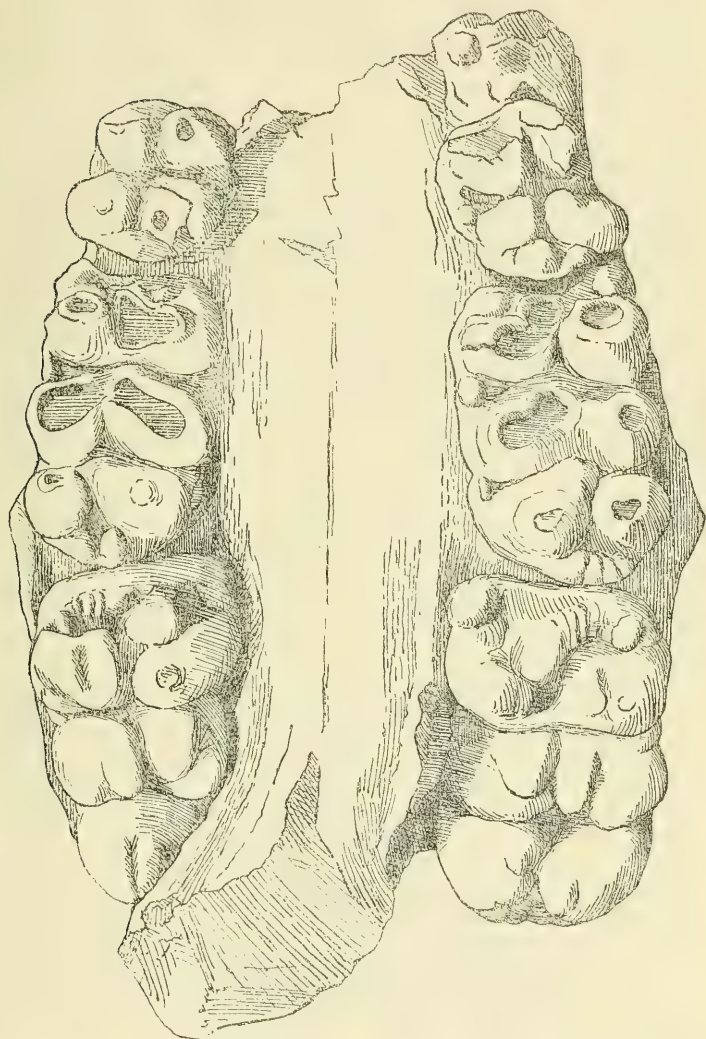
‡ Loc. cit. pl. vii. fig. 3.

§ Andrews, Phil. Trans. R. S. vol. xciv. p. 108 (1903).



division of the various cusps in the ridges is less noticeable. This, again, is apparently due to wear; the grooves between the

Text-figure 1.



*Bunolophodon angustidens*. Palate with second molars just erupting.  $\times \frac{1}{2}$ .

cusps are often not more than shallow wrinkles in the thick enamel, and very little use would be sufficient to obliterate them.



In connection with these palates, the third upper molar (Pl. I. fig. 1) may be described, of which there are two separate specimens, a right and left, both unworn and of similar pattern. They differ in shape from corresponding teeth from France in the collection of the British Museum in being broad in front and in getting narrow behind so rapidly that the ground-plan of the tooth is that of an isosceles triangle instead of the more usual elongated form.

A tooth figured by Schlesinger\* (var. *subtapiroidea*) is apparently nearer the present one in shape, but, being tilted up in the figure, his specimen cannot be closely compared. In structure the two are very similar, except that in the Indian specimens the fourth ridge (talon) consists of three cusps only instead of four, and that anything in the nature of valley cusps is conspicuous by its absence. In Schlesinger's form the cusps of the main ridges are three on each side, except on the last ridge where they are double only; in the present form they are partly double, but here and there show either the treble condition or the beginning of it. In his form, however, there is a pair of accessory cusps which, while not very conspicuous, can be seen clearly in the first two valleys. These are absolutely unrepresented in the Indian form, with the sole exception of the first valley in one of the two teeth, which has a low but distinct cusp on the outer side connected to the posterior flank of the first ridge. It is possible that the "subtapiroid" condition is the more primitive, and small mutations in the direction of greater complication of the valleys are therefore to be expected.

These third upper molars, while nearly as broad as Schlesinger's specimen, are shorter, and are considerably more so than French specimens.

Another separate upper tooth, in quite unworn condition, is here figured (Pl. I. fig. 2). It is apparently a second molar of the left side, but is rather larger than the corresponding teeth in the two palates already described. It is similar to them in all respects, except that the arrangement of the cusps is much more that of the "*typica*" form. This is especially noticeable in those of the inner side and on the second ridge, where as many as eight cusps of different sizes can be counted. At first sight this tooth might be mistaken for a very small third molar on account of its rather pointed end, large talon, and absence of posterior pressure mark. If this were really so, it might have some bearing on Pilgrim's genus *Hemimastodon*. The pointed appearance is due to the thick enamel being broken away on each side, and is therefore purely artificial; if this part be restored, the tooth has the square end of a second molar. The large talon is due to the tooth being in germ and becomes resorbed when the third molar begins to press against it; in each of the two palates in which the third molar is not yet in contact with the second the latter has a large talon.

\* Schlesinger, *loc. cit.* pl. vii. fig. 3.

Of upper premolars there are two specimens, both unworn. One, apparently a third premolar of the left side, consists of four cusps arranged in pairs, but not joined into ridges, and a small talon. This is a small tooth (Pl. IV. fig. 3) about 30 mm. long and 20 mm. in width. The other, a fourth premolar (Pl. IV. fig. 2) 45 mm. long and 36 mm. wide, is formed of two separate cusps in front, while the hinder cusps are subdivided each into about four smaller ones, and make a nearer approach to a ridge; the talon is fairly well-marked.

It may be stated at this point that no part of the material in the present collection gives any evidence in support of the genus *Hemimastodon*\*, which was originally described from specimens from the same beds in Baluchistan. Schlesinger† has criticised the validity of this genus somewhat adversely, and has pointed out that, with the exception of the type specimen (a third upper molar), all the other specimens fall within the limits of known variation of *B. angustidens*. The type tooth has only three ridges instead of four, and is of a more pronounced triangular shape than the third molars just described. Schlesinger has made the tentative suggestion that it may be a four-ridged tooth with the front ridge broken away‡, which has been misinterpreted as a complete three-ridged one. This, of course, is possible, and fractured specimens of proboscidian teeth with extraordinarily little evidence of the fractured surface are not rare. On the other hand, the broken edges of these teeth all show a convex anterior border, whereas the presumed line of fracture in the tooth under discussion is decidedly concave. The normal front border of these teeth seems to be convex in unworn specimens, which in fully-developed teeth may become flat or concave by pressure of the tooth in front. If Pilgrim's specimen be an entire one, there remain alternative explanations. Either it is an abnormal specimen, or Pilgrim was correct in making a generic distinction for it and keeping it apart from the genus *Buonolophodon*. In neither case is there any proof for or against his view, except the negative evidence of two seasons' collecting over the same ground, which has produced nothing to confirm the genus *Hemimastodon*, while the more ordinary variations of *Buonolophodon angustidens* occurred in fair quantity.

The right and left fragments of the lower jaw are in precisely the same stage of wear as the older of the two palates, and are in all probability parts of the same animal. The fourth premolar and first molar are well worn, the second has the first two ridges in wear, and a complete third molar lies in the alveolus.

Compared with a specimen in the British Museum, the mandible (text-fig. 2) is not only smaller, but gives the impression of having been considerably shallower than is usual; it compares

\* Pilgrim, *loc. cit.*

† *Loc. cit.* p. 48.

‡ A third lower molar minus the first ridge would give a shape very close to that figured by Pilgrim.

Text-figure 2.

*Bundolophodon angustidens*. Lower jaw with third molar in the alveolus.  $\times \frac{1}{2}$ .

more closely with Schlesinger's figure of a specimen\*, a rather older animal, which is named var. *subtapiroidea*, but which is noted as not typical.

The third lower molar of this present specimen agrees, however, neither with those figured by Schlesinger for var. *typica*†, nor for var. *subtapiroidea*†, nor with any of the corresponding teeth of *angustidens* in the British Museum collection or at Cambridge.

On the other hand, there are four specimens of third lower molars in the present collection which agree in a certain point among themselves and also with that described by Lydekker as the type tooth of var. *palaeindica*.

There are the usual four ridges and small talonid. Each ridge is formed of two cusps, each cusp being unequally divided into a large outer and small inner one, the two smaller cusps lying towards the middle line of the tooth, and the four cusps which constitute the ridge are arranged in a straight line at right angles to the long axis of the tooth. The only exception to the division of the cusps is that the inner cusp of the fourth ridge is practically undivided. So far these characters approximate to those of *subtapiroidea*; the first and second valleys, however, have each a large cusp standing up separately in unworn specimens from the ridges, but showing in worn specimens as being more connected to the anterior ridge than the posterior; the third valley in this specimen has no cusp visible. This arrangement does not appear to be that of Schlesinger's var. *tapiroidea*. A reference to his figures shows that it should have the valley cusps small or absent‡ and the main cusps clearly divided, while in var. *typica* the main cusps are less clearly divided and the valley cusps are prominent. There are, moreover, two cusps to each valley, the anterior being derived from the posterior flank of the external cusp of the anterior ridge, and the posterior from the anterior flank of the corresponding cusp of the posterior ridge§.

A specimen of a small form of *typica* from Sansan, in the Cambridge Museum, is figured for comparison with the Indian forms (Pl. III. fig. 1).

Either of these forms can be matched by specimens from the Middle Miocene of France in the British Museum collection. The valley cusps may be large or small, but always show the same tendency to be two in each valley. The Indian specimens all show single cusps in the valleys, large in the first, smaller in the second, and in the third valley may even be absent.

Lydekker|| states that var. *palaeindica* is separated on account of a "somewhat greater development of the accessory columns."

\* Schlesinger, *loc. cit.* pl. v. figs. 1 & 2.

† *Loc. cit.* pl. viii.

‡ This is best shown in his fig. 1 of plate viii.

§ This arrangement can clearly be seen in his fig. 4 of plate viii., where a string, used to support the specimen, runs between the two cusps in the second valley of the tooth.

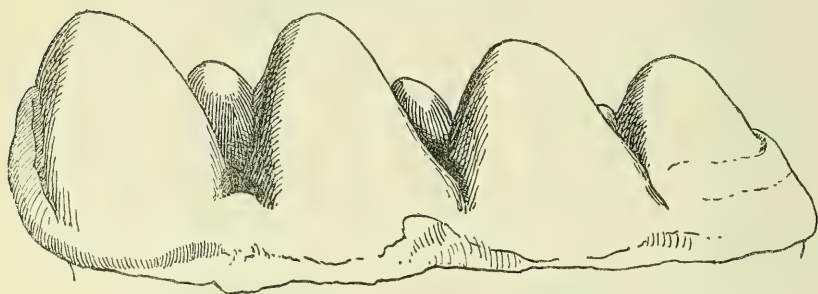
|| Cat. Foss. Mamm. British Museum, vol. iv. p. 29.



It is, however, not so much that the cusps are necessarily more developed, as that their comparative isolation from the ridges is the point that strikes the eye. And a greater character is the fact that they are single in each valley. An absolutely unworn third lower molar similar to the tooth in the jaw described above is here figured (Pl. II. fig. 1 and text-fig. 3), but being in better condition, it shows the characters more clearly.

Of European forms in the collection of the British Museum, the nearest approach in general appearance to the Indian teeth is a damaged specimen with the first ridge and front part of the second broken away (Pl. II. fig. 2). The main cusps were probably divided as in the Indian specimen, but the divisions have become obliterated by slight wear. The third ridge shows the presence of the second valley cusp, which is small but enough with the larger anterior one to close the valley. The third valley is similar to the Indian specimen in having only one cusp. The talon of the Indian specimen is very small and consists of

Text-figure 3.



*Bunolophodon angustidens*. Third lower molar in side view.  $\times \frac{3}{4}$ .

two cusps only, and this is rather a feature of the Indian teeth, which have either two or never more than three cusps on this ridge. French forms seem to have three or four cusps as in the specimen figured, while Schlesinger figures \* four molars, two of *subtapiroidea* with two cusps, one of *typica* from France with two, and one of *typica* with three. On the whole, the Indian lower teeth seem to come more under Schlesinger's heading of *typica*, while the upper teeth approach that of *subtapiroidea* †.

A larger and more worn third lower molar (text-fig. 4) is figured which shows a distinct curvature of the lateral borders. This curvature Lydekker has quoted as one of the characters of var. *paleindica*, but the presence of perfectly straight teeth in these deposits shows that it has no great significance. On the other hand, it shows very clearly that the valley cusps are single.

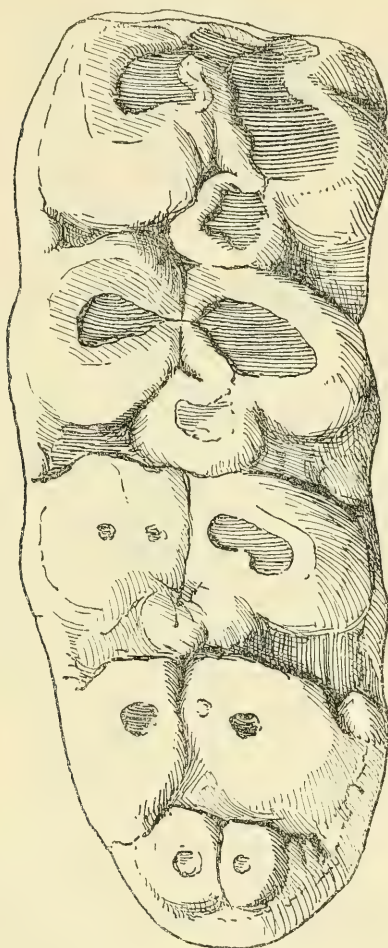
\* Schlesinger, *loc. cit.* pl. viii.

† In one case the upper and lower teeth belong to one individual, which renders his distinction of less value.



It is not unlike Lydekker's figured \* specimen (text-fig. 5), except that in the latter the cusps of the transverse ridges are not straight across, but are bent up in the middle line in the third and

Text-figure 4.



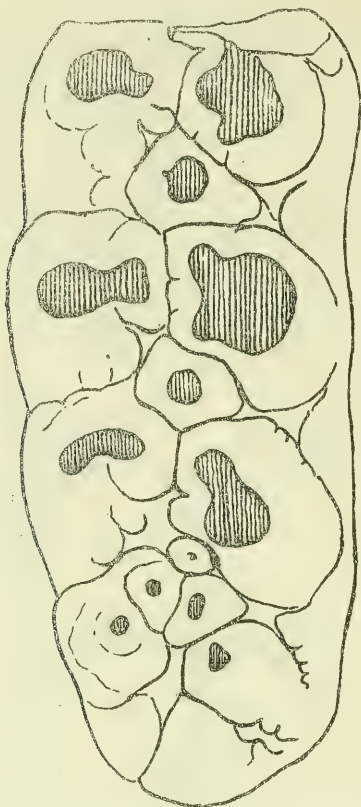
*Bunolophodon angustidens*. Third lower molar.  $\times \frac{3}{4}$ .

especially in the fourth ridges. After making allowance for this, his form can be seen to fall in with the other Indian teeth here described. As this complete singleness of valley cusps does not seem to occur elsewhere, it seems that Lydekker's view that the

\* Mem. Geol. Surv. Ind. vol. iii. pl. 4, fig. 3.

Indian specimens form a separate variety on this character is to some extent justified \*, and has at least as much to commend it, in the present state of our knowledge, as have the varieties

Text-figure 5.



*Bunolophodon angustidens*. Outline of the type-specimen of var. *palæindica*, figured by Lydekker.  $\times \frac{3}{4}$ .

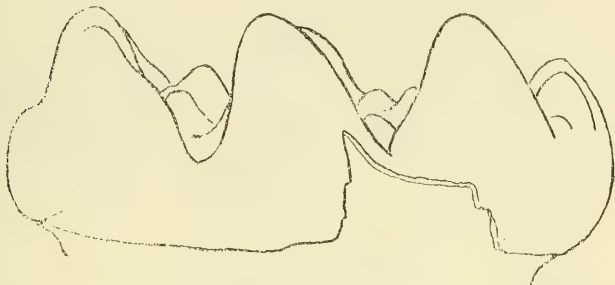
*typica* and *subtapiroidea*, which appear to have intermediate stages between them.

“Species” and “subspecies” have little significance in palæon-

\* A close approach, however, to the Indian teeth is figured by Wegner (*Palæontographica*, vol. lx. 1913, pl. xv. figs. 3 & 4). This specimen is more advanced in its larger talon, and has a number of accessory cusps in the first valley. The second and third valleys, however, are like the Indian form except that the cusps of the fourth ridge are fully divided into two each. Wegner's specimens, an upper as well as a lower molar, come from the Upper Miocene of Doppeln, and though more advanced than the Indian form, are constructed on somewhat the same plan. Wegner notices the same difference between his forms and specimens from Sansan as is noticed here.

tology except for descriptive purposes, and as other material becomes available from new sources, all these distinctions will be merged in the mass of small variations from which new mutations will eventually arise. Moreover, but few specimens of *angustidens* have, as yet, been obtained from India, and additional material is required to show whether the differences here noted are constant or not.

Text-figure 6.

*Bunolophodon angustidens*. First lower molar in side view.  $\times 1$ .

Of the other lower teeth, the second molar is rather different from a French specimen from Simorre (B.M. No. 42720) in being longer and narrower in proportion, in the more widely open valleys, and in the greater prominence of the talonid ridge, where the two cusps stand up very prominently (text-fig. 2). Of first lower molars there are several specimens, one of them (text-fig. 6 and

Text-figure 7.

*Bunolophodon angustidens*. First lower molar (B.M. No. 29671) from Simorre, in side view.  $\times 1$ .

Pl. IV. fig. 1) absolutely unworn. Compared with two specimens (text-fig. 7), also unworn, from Sansan and Simorre respectively, the Indian tooth is rather longer for its breadth and is widest at the last ridge; the valleys, as in the other lower molars, are less blocked by the accessory cusps. The talonid is formed of two

well-marked cusps, a feature of all the Indian teeth, whereas of the European forms here compared, one has three cusps and the other a low ridge of eight or nine wrinkles. The valleys are more open and the ridges lower. The accessory cusps in the second valley are much lower.

There remain for a brief notice several ends of lower teeth, apparently third molars, which are of unusual form. They all resemble the one figured (Pl. III. fig. 2) in the buckling up of the last ridge and in the curious structure of the talonid, which is formed of four cusps of different sizes pressed together into a conical hillock. The valley between the last ridge and the talonid is widely open and without any accessory cusp. This condition I have not been able to match at all closely, although some specimens of *B. longirostre* approach it. The teeth are the average size of *B. angustidens*. Whether they represent another form or are within the range of variation of the latter species cannot at present be told.

### DINOTHERIUM.

This genus was first described from India by Falconer\*, who named a specimen from Perim *D. indicum*. Its specific characters, according to him, lie in the shape of the jaw, there being no difference from *D. giganteum* in the teeth except a greater thickness of the enamel.

A second form, smaller than the first, from Attock was mentioned, but not definitely named by him. This was subsequently called *D. pentapotamia* by Lydekker†. In the Catalogue of Fossil Mammalia in the British Museum‡, presumably his final opinion on the subject, he included the two forms under the name *indicum*, and stated that many of the differences previously used by him had proved to be individual variations.

Another "species," *D. sindiense* (Lydekker), is too fragmentary to afford any evidence of a specific character.

More recently Pilgrim has mentioned this genus. In the Records § of the Indian Geological Survey he names a form from Baluchistan *D. naricum*, there stating that "it differs very markedly from the other known species," and giving certain characters. In his Memoir||, however, he withdrew this name and made the form a variety, *gajense* of *D. pentapotamia*, although Lydekker had already shown cause for making the latter the same as *D. indicum*.

Presumably Pilgrim's reasons for making his form a variety were those by which he was at first inclined to make it a species, i.e. the fact of the ridges in the last lower molar not being parallel

\* 'Falconer's Memoirs,' vol. i. p. 408.

† Pal. Ind. ser. x. vol. i. pt. 2, p. 72, pl. ix.

‡ Pt. iv. p. 11, and footnote.

§ Pilgrim, Rec. Geol. Surv. Ind. vol. xxxvii. p. 156 (not vol. xxxviii. as quoted by Pilgrim in his Memoir).

|| Pilgrim, Mem. Geol. Surv. Ind., n. s. vol. iv. no 2 (1912).

to one another, but diverging from within outwards, etc. In the same paper he gives characters in which he considers the Indian forms differ from *D. giganteum*. These are:—

1. The longitudinal ridge connecting the transverse crests in the molars is very much stronger in the Indian forms.

The present writer is unable to see this difference in specimens in the present collection, nor can the published figures

Text-figure 8.



*Dinotherium* sp. Lower jaw of left side in side view.  $\times \frac{1}{2}$ .

of Indian forms be said to show any great difference in this respect from European specimens in the British Museum collection.

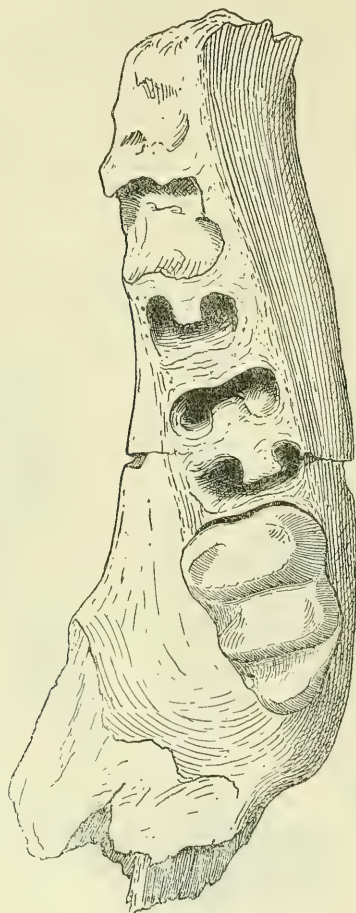


2. The transverse valley in the second upper molar is completely blocked on the inner side, and

3. The inner posterior column of the third upper premolar is more isolated than in *giganteum*, in which a ridge in continuation of this column extends right across the valley.

These two characters seem to be within the limits of variation of European forms. A third upper premolar from Darmstadt (B.M. collection, No. M. 3494) has the column quite isolated.

Text-figure 9.



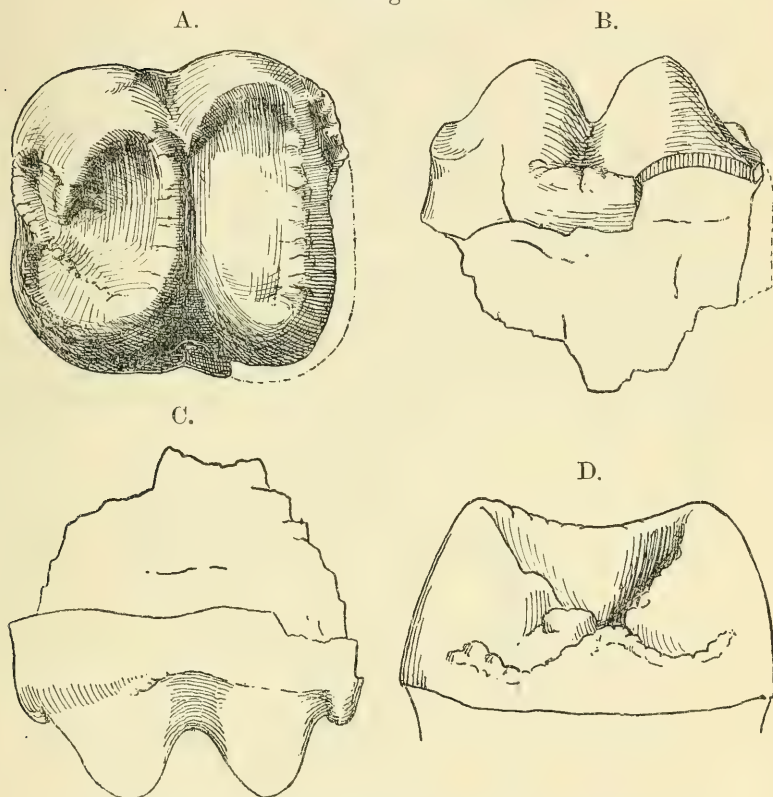
*Dinothereium* sp. Lower jaw of left side in surface view.  $\times \frac{1}{3}$ .

The material of the present collection from the Bugti beds is, as is the common experience, both scanty and fragmentary, and consists only of part of a lower jaw and some separate upper and lower teeth. The lower jaw (text-figs. 8 & 9) belongs to a small

form, and in size and structure compares closely with *D. hobleayi* \*. The third ridge of the last molar is not parallel to the front ones, but slopes at an angle similar to that found in *D. hobleayi* and *D. levius*.

Of the separate teeth, none shows any great difference from specimens of European forms with which it has been compared. An upper molar, probably a second, is here figured (text-fig. 10).

Text-figure 10.



*Dinotherium* sp. Second upper molar. A. Surface view. B. View from inner side. C. External side. D. Posterior view.  $\times \frac{3}{4}$ .

There is nothing in it which can be construed as a "longitudinal ridge," nor is there anything in the nature of a "cusp blocking the valley" which has not been found within the range of variation of European specimens. A third upper premolar (Pl. IV. fig. 6) is also figured to show the separation of the inner cusps said to be characteristic of the Indian forms,

\* Andrews, P. Z. S. 1911,

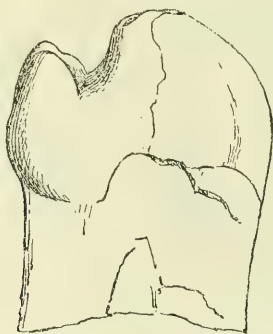
but which, as has just been stated above, occurs also in *D. giganteum*. The remaining teeth in the collection are not distinguishable from the smaller forms from Europe, and call for no comment except for three specimens. Of these, one appears to be an anterior lower milk molar (Pl. IV. fig. 4 and text-fig. 11), a tooth which apparently has not so far been noticed. It is 24 mm. long and 21 wide, and consists of two ridges, one running from the middle of the inside border round the front and along

Text-figure 11.

*Dinotherium* sp. Anterior lower milk molar, internal view from side.  $\times 1$ .

the whole outside border, but being interrupted by a small notch towards the front of the outer border; the second ridge runs transversely across the hinder part of the tooth from a high cusp on the inner side towards the outer border. The tooth is pointed in front, wide behind, and triangular in ground-plan. Posteriorly there is a small cingulum shelf and anteriorly a small cingulum cusp.

Text-figure 12.

*Sp. incertae sedis*. Side view of tooth, the anterior end pointing to the right.  $\times 1$ .

The next tooth (Pl. IV. fig. 5) is apparently a third upper premolar, but of unusual form. It is partially worn, and shows on one side two low cusps not touched by wear; opposite these are two large irregular areas of wear. There is no cingulum around these cusps, but a small one at each "end" of the tooth. In the plate the two low cusps are placed in the same position as the ectoloph of the more normal premolar (broken in this speci-



collection of the British Museum without result\*. It is certain that it does not belong to any known form of *Dinotherium*, and yet it is to teeth of that genus alone that it can be compared.

### SUMMARY.

The Proboscidea of the Bugti beds of Baluchistan consist of a form of *Bunolophodon angustidens* and a small *Dinotherium*.

The Indian *B. angustidens* is of a small type more primitive than the French forms from Sansan, nearer to Schlesinger's form *subtapiroidea* than his form *typica*, but not identical with it. Lydekker's subspecific name var. *palaeindica* may be retained for the present until intermediate forms are found to occur. The genus *Hemimastodon* is not supported by material in the collection.

The *Dinotherium* is not found to differ from the smaller European forms nor from *D. hobleyi* of Africa, and it is doubtful in the present state of knowledge whether the Indian *Dinotheres* are separable from the European.

### EXPLANATION OF THE PLATES.

#### PLATE I.

- Fig. 1. *Bunolophodon angustidens*. Third upper molar.  
 2. " " Second upper molar.  
 Both figures are reproduced about  $\frac{3}{4}$  natural size.

#### PLATE II.

- Fig. 1. *Bunolophodon angustidens*. Third lower molar.  
 2. " " Incomplete specimen from Sansan. (B.M. No. 32533.)  
 Both figures are reproduced about  $\frac{3}{4}$  natural size.

#### PLATE III.

- Fig. 1. *Bunolophodon angustidens*. Third lower molar from Sansan. (Cambridge.)  
 2. " " (*angustidens*?). Terminal part of a third lower molar.  
 Both figures are reproduced about  $\frac{3}{4}$  natural size.

#### PLATE IV.

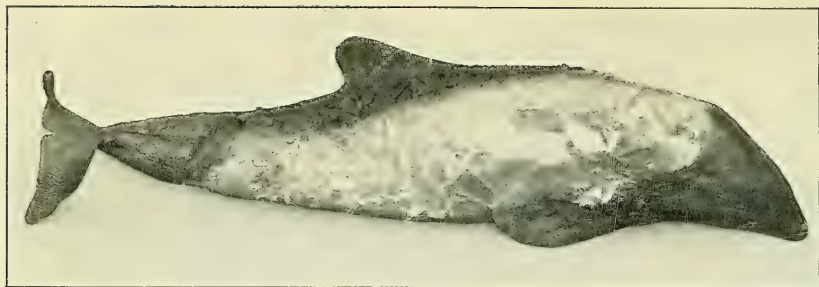
- Fig. 1. *Bunolophodon angustidens*. Unworn first lower molar.  
 2. " " Fourth upper premolar.  
 3. " " Third upper premolar.  
 4. *Dinotherium* sp. Anterior milk molar.  
 5. " " Third upper premolar.  
 6. " " ? Third upper premolar of unusual type.  
 7. *Sp. incertæ sedis*. ? An anterior premolar.  
 All figures are reproduced a shade under natural size.

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\* Such as *Listriodon* etc. India has produced animals with very unusual dentitions such as *Tetraconodon*; the present specimen may belong to yet another strange form.



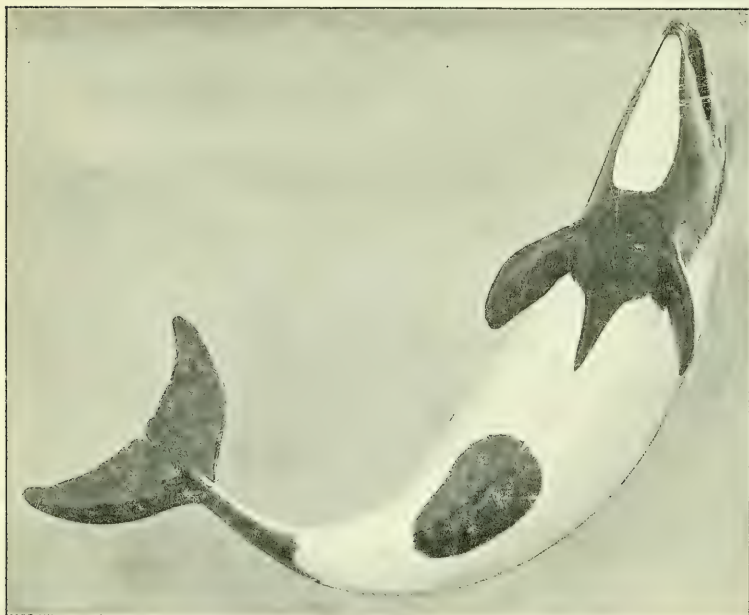




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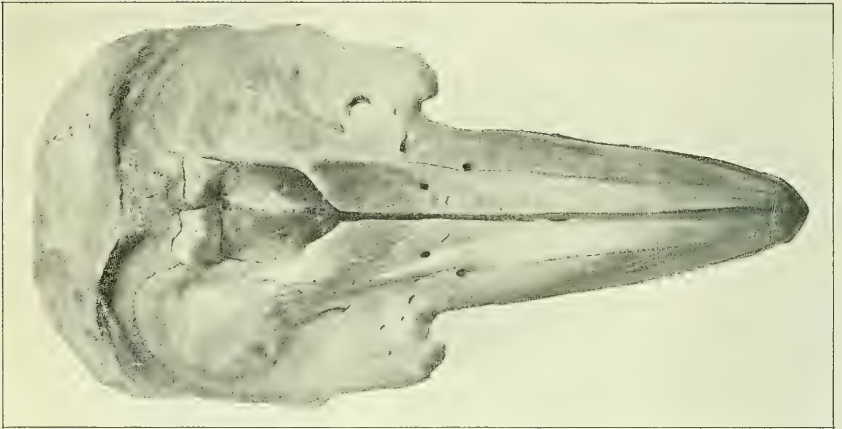


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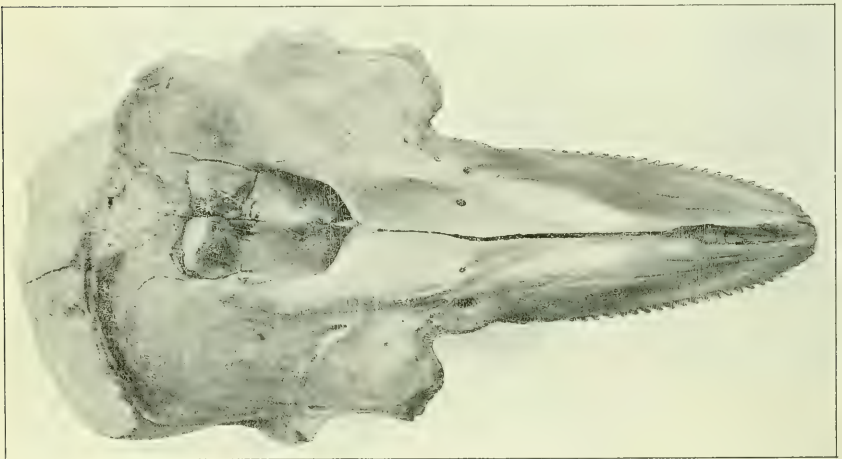




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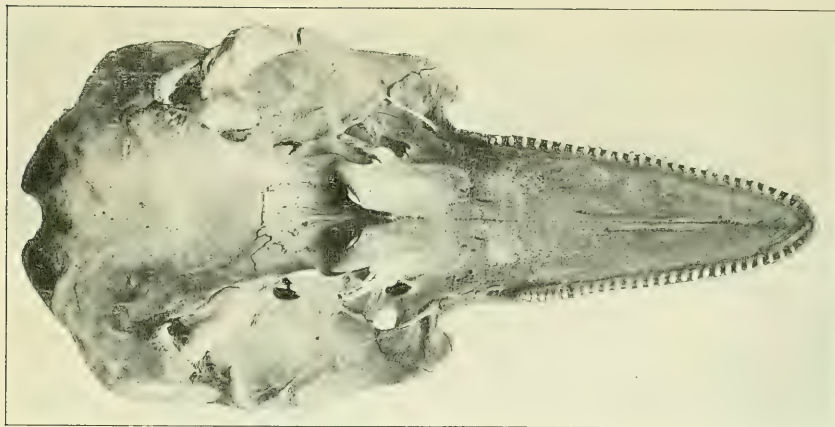
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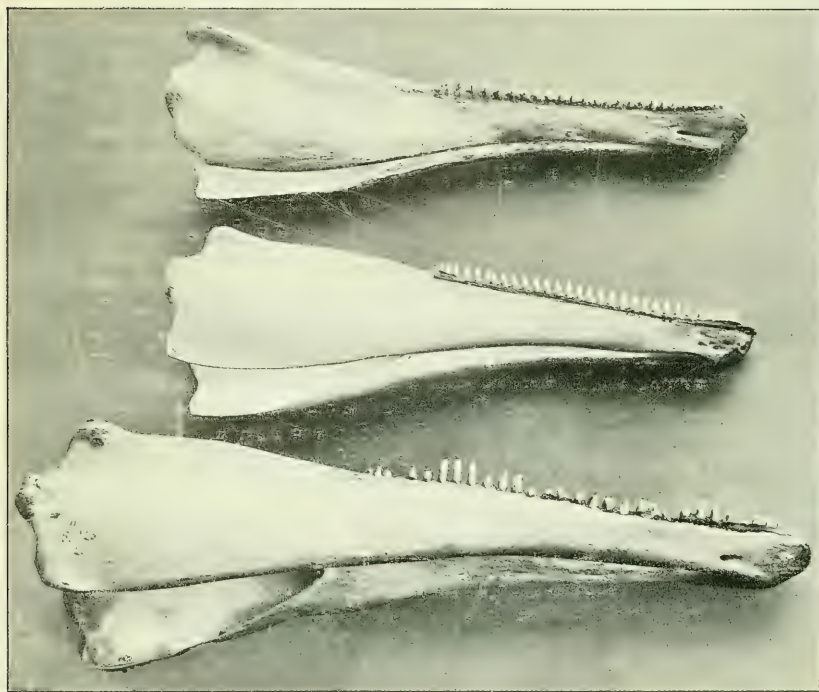
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1



2

SPECIES OF *CEPHALORHYNCHUS*.

32. On Commerson's Dolphin and other Species of *Cephalorhynchus*. By Sir SIDNEY F. HARMER, K.B.E., Sc.D., F.R.S., F.Z.S., Director of the Natural History Departments of the British Museum \*.

(Plates I-III. †)

[Received May 17, 1922; Read May 23, 1922.]

The literature of the Cetacea includes numerous specific names which are of little use to science, owing to a want of knowledge of the animals to which they were originally applied. Many descriptions are based on external features alone, while others depend exclusively on osteological characters. The correlation of these two kinds of description is difficult and often impossible, and there is probably no group which includes a larger proportion of doubtful species than could be found in a complete list of the names which have been given to Cetacea.

Under these circumstances I have felt much satisfaction in being able, as I think, to rescue one of these doubtful species from its present position. In 1804, Lacépède (pp. xlv, 317) gave a brief description of a Dolphin which had been observed by Commerson, near Tierra del Fuego and in the Straits of Magellan, during Bougainville's voyage round the world. Commerson's MSS., addressed to Buffon, by whom they were sent to Lacépède, included a diagnosis of this Dolphin:—"Tursio corpore argenteo, extremitatibus nigricantibus." It is further stated that the black colour appears only on the "extremities," and that the back and almost all the surface of the animal shine like a polished surface, white and, so to speak, silvered. These Dolphins, somewhat inferior in size to the Common Porpoise, were observed, during the Southern summer, playing round the vessel, and were described as being among the most beautiful inhabitants of the sea. They were given the name of "Le jacobite," obviously in allusion to their striking black and white colour.

Quoy and Gaimard (1824, p. 87) mention a Dolphin, "moitié blanc, moitié noir, à museau peu allongé," which they saw at the Falkland Islands. A specimen was killed, but it sank immediately. Lesson (1827, p. 181) states that during the voyage of the 'Coquille' they only once observed, at the Falkland Islands, the Black-and-white Dolphin of Quoy and Gaimard, and that every-thing authorised him to think it was the *Delphinus commersonii*.

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† For explanation of the Plates, see p. 638.

Other authors of the early part of the last century are unable to do more than quote the original account, although Gray (1846, p. 30) surmised that this Dolphin might be identical with his own *Beluga kingii*.

The external characters of the species which forms the special subject of this paper were admirably figured by Moreno (1892, pl. ix.), who described it (p. 385) under the name of *Lagenorhynchus floweri*, and gave satisfactory figures of the skull (pl. viii.). It was first observed by him, in October 1874, in the bay of the River Santa Cruz, which is on the Patagonian coast, almost in the same latitude as the Falkland Islands. It was seen in hundreds on certain occasions, but no specimen could at first be obtained, although a female, the original of the three figures of the larger individual shown in pl. ix., was secured from the same locality in December 1876, and two other specimens were obtained from Tierra del Fuego or Santa Cruz in 1884. The colour-markings were identical in all the specimens. The individual whose external measurements are recorded was 138 cm. in length, and the total length given for the skull is 28 cm.

It is unfortunate that Moreno's specific name, which was based on a good and well-illustrated account of external and cranial characters, cannot be accepted. It must be regarded, I think, as a synonym of *Delphinus commersonii*, which, although described inadequately and without illustrations, appears to be perfectly recognisable in the light of the evidence now available. Not only were Commerson's and Moreno's specimens from substantially the same locality, but the silvery colour, with black confined to the "extremities," described by the earlier observer, is equally noticeable in Moreno's figures, which represent an animal mainly white, with the head, tail, flippers, and dorsal fin black.

The only other actual description of this animal with which I am acquainted is that of the late Dr. W. S. Bruce (1915, p. 500, pl. i.), who shows the external characters of a specimen, 4 ft. 4 in. in length, which was obtained by him in 1893 at Port Stanley, Falkland Islands. It was referred, doubtfully, to *Lagenorhynchus cruciger* (d'Orb. & Gerv.), and it was styled the "Piebald Porpoise." Dr. Bruce records a number of positions to the south of the Rio de la Plata at which Dolphins believed to be "Piebald Porpoises" were observed from the ship.

It is shown by the records of Moreno and Bruce, as well as by the new evidence now submitted, that a Porpoise characterised by its strongly contrasted black and white colours arranged in a very definite pattern, is common in the neighbourhood of the Falkland Islands and of Tierra del Fuego. I think there can be no doubt that this Porpoise belongs to the same species as the "Jacobites" which played round Bougainville's ship in the Straits of Magellan, and were observed later at the Falkland Islands by Quoy and Gaimard, and by Lesson.

Liouville (1913, p. 165), in a discussion, under the heading of *Lagenorhynchus fitzroyi*, of certain Dolphins which have been recorded as *L. cruciger* or by other names, comes to the conclusion that a number of conspicuously marked Southern Dolphins, recorded under various specific names, are colour-varieties of a single species. Whether this view be correct or not, the concordant evidence derived from several distinct sources, with regard to Commerson's Dolphin, shows that this species at least is remarkably constant in the position of its areas of black and white. It may be suggested that these striking markings have the protective value which has been ascribed to the "disruptive" type of coloration in animals. As seen in the water, the white area probably divides the body into two parts which seem to have little, if any, connection with one another. The Dolphin is, in fact, effectively camouflaged, and perhaps the protection is specially successful in water liable to contain floating ice. The principal enemy of Commerson's Dolphin is probably *Orcinus*, the Killer Whale.

The British Museum has recently received the following material, referable to the genus *Cephalorhynchus*, in which I place *Delphinus commersonii* Lacép. (= *Lagenorhynchus floweri* Moreno and *L. cruciger* Bruce, *nec auctt.*):—

A. An eviscerated male specimen (in salt), 4 feet 6 inches long, captured in Stanley Harbour, Falkland Islands; presented by Mr. J. E. Hamilton, Magistrate of West Falkland, who stated that the stomach contained "krill" (the Norwegian whalers' name for the small Crustacea which form the food of Whalebone Whales) and the pens of cuttlefish. The vertebral epiphyses are quite free, and the animal was accordingly immature.

B. A skull, with lower jaw, picked up on the shore of Byron Sound, West Falkland; presented by Mr. Rupert Vallentin.

C. Two photographs of a specimen stranded in the Falkland Islands on another occasion; presented by Mr. Rupert Vallentin, who stated that these Porpoises are fond of basking in the beds of *Macrocystis* when the sun is shining, and that he knew of no other species in that locality.

D. A note-book, lent by Mr. Lionel E. Adams, containing observations on Dolphins observed by him from a ship in the Straits of Magellan, together with a small photograph showing two of them in the air during a jump out of the water. The note-book included an excellent sketch, completely agreeing with A and C, and the passage "Jet black and pure white (no shades). I did not see any variation in the markings of one of the hundreds that played about the ship."

The following notes were made on Mr. Hamilton's specimen (Pl. I. figs. 1 & 2) before its skeleton was prepared. The skin, although somewhat abraded, showed the external coloration perfectly distinctly.



*Colour*.—Jet-black and pure white, the principal white area shading to some slight extent through grey to the black areas in front and behind (as in Moreno's pl. ix. fig. 1), but the junctions of the two colours otherwise very sharply marked. The black occurred on the whole of the head and lower jaw (interrupted ventrally by a pear-shaped, median, white area on the throat), extending backwards obliquely from the sides of the head to the pectoral fins, which were black on both surfaces, and was continued across the ventral side as a broad band, behind the white marking on the throat, this band giving off an acutely pointed median prolongation backwards, between the flippers. The tail, including the flukes on both surfaces, was black all round, for nearly a foot from its emargination, and this colour was continued forwards obliquely on the back beyond the dorsal fin, but separated by a white interval even in the mid-dorsal line from the black of the head. A large heart-shaped black area surrounded the reproductive opening, and was observed by Mr. Hamilton in another male specimen examined by him. The white part of the skin consisted of (a) the median ventral area on the throat, (b) the main white area encircling the body obliquely, much more developed ventrally than dorsally, and including most of the ventral and lateral regions of the body.

Mr. Vallentin's photographs (Pl. I. fig. 3; Pl. II. fig. 1), one of which shows that the specimen was a male, correspond in every essential detail with the above description. Mr. Adams's sketch (D), which represents animals seen in the sea, agrees closely with the others, but from the conditions under which it was made, it is not surprising that it does not show any black area round the reproductive opening. His photograph shows two living animals in the air, as seen from the ship, and it suggests the idea of a Porpoise "*moitié blanc, moitié noir*," as described by Quoy and Gaimard.

Neither Moreno nor Bruce shows a *broad* black marking round the reproductive opening. Moreno's ventral view indicates, however, a narrow, longitudinal, black mark in this situation, its posterior third being nearly constricted off from the front portion. The specimen was a female, and the question arises whether the individuals of this sex normally have a ventral black marking narrower than that of the male. One of Bruce's figures (the lowest in the Plate) of an animal of unrecorded sex gives some indication of a constricted, narrow marking like that shown by Moreno.

*External form*.—The head of A had no beak distinctly outlined from the remaining portion, but was nearly conical. The dorsal fin had an elongated base, and was low and rounded, with but little indication of a falcate shape. The flippers were also more rounded at their ends than in most Dolphins. These characters point to *Cephalorhynchus* (cf. True, 1889, pp. 108, 176), and this conclusion is confirmed by the cranial characters.



*External measurements of Mr. Hamilton's specimen (A):—*

	Cm.
Total length .....	137*
Dorsal fin (middle) to tip of snout .....	81
„ „ ( „ ) to emargination of tail .....	63·5
„ „ length of base .....	22·8
Flipper, length, from axilla .....	16·5
„ „ inferior border .....	23·5
Gape, length of, from tip of upper jaw ...	16·5
Snout to blow-hole.....	20·3
Tip of lower jaw to (middle of) umbilicus..	64
Umbilicus to reproductive aperture † .....	14
Reproductive aperture to anus.....	18·5
Anus to emargination of tail .....	40·5

The characters of *Cephalorhynchus* Gray were re-defined by Flower, in his well-known paper on the Delphinidæ (1883, p. 473), the type-species being *Delphinus heavisidei* Gray, 1828. In his Review of the Delphinidæ, True (1889, pp. 108, 176) recognises four species of the genus—the type-species from the Cape of Good Hope, *C. albifrons* True and *C. hectori* Van Beneden from New Zealand, and *C. eutropia* Gray from Chili. In 1893 and 1896 several new Dolphins from Chili were described by R. A. Philippi. His two papers were later criticised by True (1903), who expressed the opinion that *Phocœna* or *Tursio albiventris* (Perez, MSS.) Philippi, 1893, 1896, is a synonym of *C. eutropia*, and that *Tursio platyrrhinus* Philippi, 1896, is probably the same species. *Tursio* ? *panope* ‡ Philippi, 1896, was not thought by True to be referable to *Cephalorhynchus*, but it seems possible that it may also belong to this genus.

The external characters have been described in *Cephalorhynchus heavisidei*, *C. albifrons*, *C. hectori*, and *C. albiventris*. *C. eutropia*, *C. platyrrhinus*, ? *C. panope*, and ? *C. chiloënsis* are known from cranial characters alone.

The British Museum possesses the type-specimens of *C. eutropia* § and *C. heavisidei*. The skull of the latter was inside the mounted skin when Flower wrote his revision of the Delphinidæ in 1883. It has since been removed, and although defective in the occipital region, it is otherwise in good condition. The following table gives measurements of the skulls in the Museum :—

\* The measurement recorded by Moreno is 138 cm., and that given by Bruce is 132·2 cm.

† The distances between the apertures were in each case measured from their middle points.

‡ Philippi (1901) later described a new Dolphin, *Tursio* ? *chiloënsis*, from Chili, which he stated to have resemblances to *T. panope*.

§ Figured by Gray 1846, pl. xxxiv. figs. 1, 2; see also Gray, 1866, p. 262.

	<i>C. entropia</i> Type, 936a = 49.5.25.2.	<i>C. commersonii</i> .		<i>Cf. Flower</i> P. Z. S. 1883, p. 506.
		A. Falkland Is. J. E. Hamilton.	B. Falkland Is. R. V. Vallentin.	<i>C. heavisidei</i> Type, 41.17.32.
1. Total length (centimetres).....	36.3	29.8	29.5	29.0 <sup>85</sup>
2. Rostrum, length .....	19.5	14.0	14.0	13.2
3.   "   width at base .....	8.3	7.3	6.5	6.8
4.   "   "   opposite 2nd tooth from hind end .....	7.7	6.5	6.2	5.9
5.   "   "   at middle .....	7.0	5.3	5.2	5.1
6.   "   vertical depth, at middle of tooth-row .....	1.7	1.6	1.6	1.5
7. Tooth-row, length of .....	16.8	12.3	12.3	11.6
8. Maxilla, right, posterior expansion of, length .....	10.5	10.9	11.2	10.4
9.   Do.       do.   width (middle of orbit to nares) .....	6.5	6.2	6.0	5.1
10. Do. width at posterior end of tooth-row .....	2.2	1.6	1.5	1.3
11. Premaxilla, right, width at posterior end of tooth-row ...	1.7	1.8	1.5	1.8
12.   "   "   width behind nares ...	...	...	...	1.2
13. Orbital width (at front of orbit) .....	15.1	12.7	12.4	12.9
14. Glenoid width .....	16.7	14.6	14.8	14.5*
15. Greatest height of skull .....	14.3	13.2	13.2	13.0*
16. Mandible, length .....	30.0	23.0	23.0	22.8
17.   "   condyle to posterior end of tooth-row .....	13.5	10.8	11.0	11.0
18.   "   depth, at middle of 17 .....	5.8	4.8	4.6	4.3
19.   "   "   at posterior end of tooth-row .....	3.7	3.3	2.9	2.6
20.   "   "   at middle of tooth- row .....	2.2	1.9	1.7	1.5
PERCENTAGES.				
1. Total length .....	100.0	100.0	100.0	100.0
2. Rostrum, length .....	53.7	47.0	47.5	45.5
4.   "   width opposite 2nd tooth from behind .....	21.2	21.8	21.0	20.4
7. Tooth-row, length of .....	46.3	41.2	41.7	40.0
8. Maxilla, right, posterior expansion, length .....	29.0	36.5	38.0	35.9
9. Maxilla, right, posterior expansion, width .....	17.9	20.8	20.4	17.6
18. Mandible, depth, middle of part behind teeth .....	16.0	16.1	15.6	14.8

\* Estimated (skull imperfect).

The external characters of Mr. Vallentin's Dolphin were not definitely known, although he himself had no doubt that the skull belonged to the species shown in his photographs. Com-

parison of the skull with the other Falkland Is. specimen confirms this conclusion. The only difference of importance is that the rostrum of Mr. Vallentin's specimen (B) is distinctly narrower at its base than is that of Mr. Hamilton's skull (A). Flower (1883, p. 469) stated that the rostrum becomes longer and wider, in proportion to the brain-case, in older Dolphins. The skull B has an unfinished appearance in the region of the base of the rostrum, as if growth were there incomplete; and the notches in the maxillæ are wider than in A. The two skulls are practically alike in their orbital width, and by an addition to the rostrum at its base, B would become similar to A in the width of this structure and in the reduction of the maxillary notches.

*C. eutropia* and Philippi's three species *albiventris*, *platyrhinus*, and *panope* agree with one another in having a rostrum which in length exceeds 50 per cent. of the total skull-length. The tooth-row is also relatively long in the same species, the percentage in *C. eutropia* (type) being 46·3, as shown by the preceding table, and ranging from 46·0 to 51·5, as shown by Philippi's measurements, in the other three species. *C. commersonii* agrees with *C. heavisidei*, and differs from the other four species, in having a rostrum less than half the length of the skull, and a shorter tooth-row, not exceeding 42 per cent. of the skull-length. The skulls of the two species are also absolutely smaller (29–30 cm.), *C. eutropia* having a skull more than 36 cm. long, and those of Philippi's three species ranging from 33·0 to 39·5 cm.

Although *C. commersonii* has a considerable resemblance to *C. heavisidei* in cranial characters, I have noted the following differences in the skulls available for comparison (Pl. II. figs. 2 & 3). The skull of *C. heavisidei* has previously been figured by Schlegel and by Van Beneden and Gervais, as pointed out below; and that of *C. commersonii* by Moreno (1892, pl. viii.).

*Premaxilla*.—The outer edge of this bone, in *Cephalorhynchus* generally, forms a prominent elevated ridge in front of the anterior nares (Flower, 1883, p. 473). In *C. commersonii* the left bone is not prolonged behind this ridge, that of the right side forming a slender splint passing towards the nasal of its side, but not reaching it. Moreno's fig. 1 *a* seems to agree in this respect. In *C. heavisidei* this posterior process is considerably larger in the left premaxilla, and still larger in the right bone, where it is 12 mm. wide and touches the nasal, passing back to about the middle of its length. *C. eutropia* resembles *C. heavisidei* in these respects, except that the right premaxilla does not reach the nasal, from which it is 11 mm. distant. The floor of the depressed triangle in the premaxillæ, in front of the anterior nares, is flatter in *C. commersonii* than in *C. heavisidei*, where it is slightly concave. The width of the premaxillæ in the front half of the triangle is distinctly greater in *C. heavisidei* than in the other species, and the maxillæ are here correspondingly narrower.

*Maxilla*.—*C. commersonii* seems to be characterized by the specially large posterior expansions of the maxillæ. Measuring the length of these expansions from the bottom of the maxillary notches along a line parallel with the middle line of the skull, and the breadth as indicated in the table of measurements, these parts are absolutely longer in *C. commersonii* than in the considerably larger type-skull of *C. eutropia*. In *C. heavisidei* they are relatively narrow, and do not completely cover the orbit, the whole upper margin of which is visible in a dorsal view, with part of the postorbital process, which slopes a good deal outwards.

In *C. commersonii*, the front of the orbit is completely concealed by the maxillary expansions, the only part visible dorsally being the postorbital process, which is more vertical than in the other species. Rather more of the upper surface of the orbit is shown in Moreno's figures, particularly in fig. 2, which is described as representing a younger specimen; and the extent of the overgrowth of the orbit by the maxilla is perhaps dependent on age.

In *C. heavisidei* there is a slight constriction of the outer margin of the rostrum, 20 mm. in front of the maxillary notches, so that a small lateral lobe is partially marked off at the base of the rostrum, on each side. These lobes do not occur in *C. commersonii*.

*Nasal*.—These bones, though no doubt variable, show certain features which may be distinctive. In *C. heavisidei* they are subdiscoidal, the central part the thickest and the margin thinner, and they are in contact with one another, on the upper side only, for about 7 mm., leaving a small triangle of the frontals uncovered between their lower borders and the mesethmoid. The greatest diameter is 25 mm. In *C. eutropia* each bone is quite twice as wide as long (25, 11 mm.), and has a sharply marked, nearly vertical, anterior face, which almost reaches the mesethmoid. The left nasal is wanting in skull B of *C. commersonii*, and the right nasals are not altogether alike in the two skulls. The shape seems to be somewhat intermediate between those of the other two species, being more quadrangular than in *C. heavisidei*, and rather longer in proportion to the width than in *C. eutropia*, the two bones having a median suture nearly reaching the mesethmoid. The right nasal of skull A measures 22 mm. in width and 17 mm. in length. Moreno's fig. 1a gives similar evidence.

*Mandible* (Pl. III. fig. 2).—While differing in certain respects, all three species show, more or less distinctly, the outwardly bowed rami, corresponding with the expanded part of the rostrum, given by True (1889, p. 108) as a generic character. That of *C. eutropia* (c) is much larger and heavier than those of the other species, but it resembles the mandible of *C. commersonii* (b) in general form and in the shape of its coronoid process, which is a blunt triangle with its apex directed nearly vertically and lying



well in front of the condyle. In *C. heavisidei* (*a*) the coronoid process is directed backwards, so that its apex lies but little in advance of the condyle, while from its front end the upper edge of the jaw slopes down to the teeth, instead of remaining at first horizontal, as in the other two species; and the jaw is slighter and has less vertical depth than in them.

*Pterygoid*.—The importance of these bones in distinguishing genera in the Delphinidæ was pointed out by Flower (1883), who relied on Van Beneden and Gervais' figure (pl. xxxvi. fig. 1*a*) for evidence as to *Cephalorhynchus*, and reproduced it on p. 473. There can be no reasonable doubt that the figure was drawn from a skull with incomplete pterygoids, and it is thus to some extent misleading. The type-skull of *C. heavisidei* resembles the figure as reproduced by Flower, in respect of the pterygoids, but a comparison with the two skulls of *C. commersonii*, in both of which these bones are complete, shows that they are much longer than would be inferred from that figure. They resemble in shape the pterygoids shown by Flower (1883, p. 471) in *Globicephala* (*Globiceps*), but their posterior margin is more oblique, or less nearly transverse. In skull A (Pl. III. fig. 1), the palatal surface of each pterygoid measures 36 mm., from the point where it leaves the vomer, to its posterior tip. In their free, posterior portions the two bones are separated by a narrow,  $\Pi$ -shaped interval, 18 mm. long and widening to 8 mm. across, at the commencement of the posterior oblique borders. Skull B is similar, except that the interval between the free parts of the pterygoids is  $\Lambda$ -shaped, and the length to the tip is only 30 mm. The pterygoids are incomplete in Moreno's figure.

*Teeth*.—Skull A (*C. commersonii*) has  $\frac{29-29}{30-30}$  teeth visible without cutting away any of the gum. One or two small ones may perhaps be present, beneath the gum, at the anterior end of the series. In skull B, in which many of the teeth are wanting, the number is about 29 on each side of each jaw. In *C. heavisidei* (type), the number is  $\frac{27-27}{26-26}$ , while in *C. eutropia* (type) it is 30-31 on each side of each jaw.

The osteological features of the Cetacea are so variable that it is often impossible to be sure how far characters selected from an examination of a limited amount of material are of any value. It is thus important to point out that, in the features enumerated above, the two skulls of *C. commersonii* are in substantial agreement with one another, except where attention is called to a difference. There is evidence, moreover, that other specimens of *C. heavisidei* agree with the type-skull. The skull of this species has been figured and briefly described by Schlegel (1841, p. 31, pl. iii. figs. 1, 4; pl. iv. fig. 6); and by Van Beneden and Gervais (1868-1879, p. 599, pl. xxxvi. figs. 1-1*b*), from a skull in the Paris Museum. The latter authors were inclined to regard the specimens of *Cephalorhynchus* from various southern localities



as belonging to a single species. I have to thank Prof. R. Anthony for the information that the skull figured in the 'Ostéographie' (figs. 1, 1 *a*) is from the Cape of Good Hope, Dussumier, 1827, although he thinks that the lower jaw figured (1 *b*) may not be from the same specimen. It may no doubt be assumed that Dussumier's specimen at least belonged to *C. heavisidei*.

The following may be noted as points of agreement between the type-skull of *C. heavisidei* and Schlegel's figures:—The small lateral lobes at the base of the rostrum on each side; the narrow posterior expansions of the maxillæ, not completely covering the orbit; the shape of the nasals, which do not quite touch one another and leave a triangular part of the frontals exposed between themselves and the mesethmoid; and the broad posterior ends of the premaxillæ, both of which nearly reach the nasals. In Van Beneden and Gervais' figure most of these resemblances are also noticeable, and attention may be specially directed to the right premaxilla, which reaches the nasal behind.

CEPHALORHYNCHUS Gray, 1850 (see Flower, P. Z. S. 1883, p. 473, and True, 1889, Bull. U.S. Nat. Mus. no. 36, pp. 108, 176).

*C. COMMERSONII* Lacép.

*Delphinus commersonii*, "Le Jacobite," Lacépède, 1804, Hist. Nat. Cét. pp. xliv, 317 (referred to by Quoy and Gaimard, 1824, Voy. 'Uranie,' p. 87; and by Lesson, 1827, Voy. 'Coquille,' p. 181).

*Delphinus commersonii* Desmarest, 1822, Mamm. 2<sup>e</sup> Partie, p. 517.

*Phocæna commersonii* Lesson, 1827, Man. Mamm. p. 414.

*Lagenorhynchus floweri* Moreno, 1892, Rev. Mus. La Plata, iii. p. 385, pls. viii., ix.

*Lagenorhynchus cruciger*? Bruce, 1915 (*nec auctt.*), "Piebald Porpoise," Scotia Rep. vol. iv. p. 500, pl. i.

*Known localities*.—Tierra del Fuego, Straits of Magellan, coast of Patagonia, Falkland Islands.

*External characters*.—Length at least 140 cm. Head conical, without distinct beak. Dorsal fin bluntly triangular, not falcate. Flippers rounded at the end, not falcate. Most of the sides and ventral surface silvery white, this colour extending completely across the back, between the head and the dorsal fin. A large white, median, pear-shaped area, widest behind, on the throat. Head, tail, caudal, pectoral, and dorsal fins jet-black (the fins on both surfaces), a narrow dorsal band of black passing obliquely from the tail to just beyond the dorsal fin, a broad black band extending across the ventral side between the flippers, produced backwards into a median, acuminate process. A black area surrounding the reproductive opening. White and black areas very sharply defined. Visible teeth 29–30 on each side of each jaw.

*Skull*.—Total length at least 29–30 cm. Rostrum about 47 per cent. of the total, at base half as wide as long, without projecting lateral lobes posteriorly. Tooth-row 41–42 per cent. Posterior lobes of maxillæ large, almost completely covering the orbits; the postorbital process nearly vertical and hardly visible from above. Premaxillæ little prolonged behind the anterior nares, the floor of the depressed triangle flat. Nasals subquadrangular, meeting in a median suture, the width much less than twice the length. Pterygoids separated behind by a  $\Pi$ - or  $\Lambda$ -shaped interval; the posterior border oblique, its tip 30–36 mm. from the vomer. Upper border of mandible horizontal, behind the teeth, the coronoid process bluntly triangular.

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## EXPLANATION OF THE PLATES.

## PLATE I.

*Cephalorhynchus commersonii*.

Figs. 1 & 2. Mr. J. E. Hamilton's eviscerated specimen (A), lateral and ventral views.  $\times \frac{1}{4}$ .

Fig. 3. Ventral view of another individual (C). From a photograph sent by Mr. R. Vallentin.

## PLATE II.

*Cephalorhynchus commersonii*.

Fig. 1. Side view of specimen C. From a second photograph sent by Mr. R. Vallentin.

Fig. 2. Skull of specimen A, dorsal view.  $\times$  about  $\frac{1}{3}$ .

*C. heavisidei*.

Fig. 3. Skull of the type-specimen, dorsal view.  $\times$  about  $\frac{1}{3}$ .

## PLATE III.

*Cephalorhynchus* spp.

Fig. 1. *C. commersonii*. Skull of specimen A, ventral view.  $\times$  about  $\frac{1}{3}$ .

Fig. 2. Lower jaws, from the right side.  $\times$  about  $\frac{1}{3}$ .

a. *C. heavisidei*. Type-specimen.

b. *C. commersonii*. Specimen A.

c. *C. eutropia*. Type-specimen.

33. The Comparative Anatomy of the Tongues of the Mammalia.—VII. Cetacea, Sirenia, and Ungulata. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society.

[Received April 18, 1922: Read May 9, 1922.]

(Text-figures 25–30.)

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INTRODUCTION.

In papers \* on the tongues of the Primates, I showed that the mobility is well marked, the gustatory and secretory organs are well developed, and the papillæ are not specialised for one kind of food. In the remaining mammalian orders one or more of these characters is highly developed, or greatly diminished, in accordance with the nature of the diet and mode of feeding. As the literature contains many descriptions of individual tongues, the remaining papers of this series will be limited to general descriptions of the different types, and special attention will be paid to physiology and classification.

The present paper is based on the examination of specimens in the Society's Prosectorium, the British Museum (Nat. Hist.), and the Museum of the Royal College of Surgeons.

Order CETACEA.

*List of specimens examined.*

Suborder MYSTACOCETI (Baleen Whales).

Pieces of tongue of *Balæna* and *Balænoptera*.

Suborder ODONTOCETI (Toothed Whales).

Sperm Whale (*Physeter macrocephalus*), Sowerby's Beaked Whale (*Mesoplodon bidens*), Beluga (*Delphinapterus leucas*), Porpoise (*Phocaena communis*), *Cephalorhynchus eutropia*, Risso's Dolphin (*Grampus griseus*), Common Dolphin (*Delphinus delphis*), Bottle-nosed Dolphin (*Tursiops tursio*), White-beaked Dolphin (*Lagenorhynchus albirostris*).

\* P. Z. S. 1922, pp. 1–29, 277–322, 497–524, 741–767.

The tongues of the Odontoceti differ greatly from those of the Mystacoceti, and both differ considerably from those of the other mammalian orders. Some are so simple that they resemble the tongues of fishes.

*Size*:—In many Cetacea the tongue fills the space between the halves of the mandible, but it does not do so in the Narwhal (*Monodon monoceros*), *Balenoptera borealis* (29), and *Delphinapterus leucas*. Barclay (2) showed that the food must pass far back to reach the tongue, if it is an organ of taste in the latter. In *Balenoptera boops* (10) it forms a large mass, projecting upwards between the baleen plates like an intermolar eminence. The bulk may be so increased by gaseous decomposition after death that the tongue protrudes from the mouth. This protrusion, however, does not take place in the Odontocete tongue.

*Consistence*:—In the Odontoceti the tongue is firm, hard and muscular, and the upper surface feels like parchment. In the Mystacoceti, on the other hand, it is soft, from the presence of a large amount of oil or fat which, according to Owen (27), separates the mucous membrane from the muscles. Schulte (29) has also shown that masses of fat separate the muscoli genioglossi in *Balenoptera borealis*. The oil will exude from the cut surface of the tongue for a long period in preserved specimens. Some have, in fact, likened the tongue to a sac of blubber. Rawitz (28) and Eschricht (13) described the fat in adult animals, and Kükenthal (21) saw it in a 117.5 cm. fœtus of *Balenoptera musculus*.

*Mobility*:—John Hunter (20) showed that the tongues of the Odontoceti are more muscular and mobile than those of the Mystacoceti, and attributed the difference to the methods of feeding. In the former they are organs of prehension, but they are passive in the latter, for the food flows into the open mouth. Scoresby (31) described the mode of feeding in *Balena mysticetus* as follows:—"When the whale feeds, it swims with considerable velocity under water, with its mouth wide open; the water enters by the fore part, but is poured out again at the sides, and the food is entangled and sifted, as it were, by the whalebone, which does not allow anything to escape."

In the Odontoceti the mobility varies. In *Orcella brevirostris* (1) it is great, for the free part extends back as far as the fourth interdental space. In *Platanista gangetica* the apex is bound to the mandibular symphysis by a fold of mucosa, but the edges are free and mobile. The animal is blind and burrows in the mud at the bottom of rivers for small fishes and crustacea, which constitute its diet. So the sensitive edges of the tongue may be organs of exploration. In *Mesoplodon bidens*, according to Turner (34), the tip is mobile from side to side.

In both suborders the tongue is more mobile in the new-born animal than in the adult.

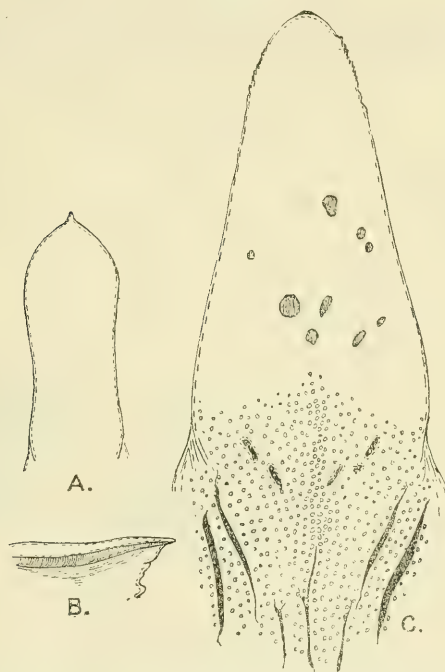
*Shape*:—The tongue is large and shapeless in the adult *Balenoptera boops* (10), but it is broad and squat in the fœtal



*Balenoptera borealis* (29). In the majority of the Odontoceti it has the usual mammalian form, but it is slipper-shaped in *Grampus griseus* and *Lagenorhynchus albirostris*.

The apex varies considerably. It is full and rounded in *Balcena* and *Balenoptera*. In the Odontoceti, on the other hand, it is not so full and rounded, and it may or may not have processes and warty growths. In *Globicephalus melas* (25), *Cephalorhynchus eutropia* (text-fig. 25 B), and *Physeter macrocephalus* (text-fig. 25 A) it is plain and pointed. In *Grampus griseus*

Text-figure 25.



Tongues of the Cetacea. A: dorsum of the tongue of a fetus of *Physeter macrocephalus*; B: lateral view of the same, showing the loose wrinkled frenum; C: tongue of *Cephalorhynchus eutropia*.

(text-fig. 26 A), *Lagenorhynchus albirostris* (text-fig. 26 B), and *Delphinus delphis* (text-fig. 26 C) it is broader and smooth, but Carus and Otto (8) described and figured it as covered with tubercles in the latter. The apical lobules are small in *Phocæna communis* (text-fig. 27 A), large in *Delphinapterus leucas* (text-fig. 27 B), and in two rows in *Tursiops tursio* (text-fig. 27 C).

The lateral borders are immense and massive in *Balenoptera boops*, and thin in the foetal *B. borealis*. They are very variable in the Odontoceti. In no Cetacean have they any lateral organs.

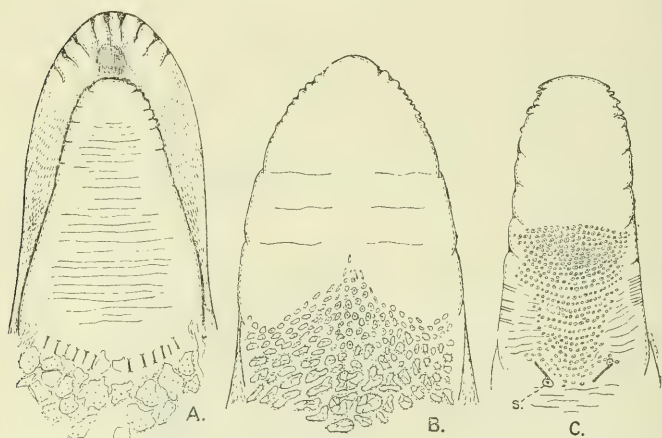
Owen (27) stated that they are plain in the Mystacoceti, but Wyman (35) described lobules in *B. borealis*. Schulte (29), however, did not figure them in the fœtus of that species.

It is difficult to decide where the oral and pharyngeal parts of the tongue meet in many species, for vallate papillæ are frequently absent. In *Orcella fulminalis* the base is delimited by a sulcus, whose ends correspond to the angles of the mouth. And many glands open into the sulcus (1).

*Sulci*:—Median dorsal and median ventral sulci are absent in most cases. But many fine longitudinal and transverse sulci may be present. In *Orcella* they feel gritty to the touch.

The tongue may be smooth and plain all over, as in the fœtal *Balenoptera borealis*. It is wrinkled all over in *Orcella brevirostris*. In many species the posterior part of the dorsum is

Text-figure 26.



Tongues of the Cetacea. A: *Grampus griseus*; B: *Lagenorhynchus albirostris*; C: *Delphinus delphis*; s: glandular sac.

divided into areas by sulci. The inferior surface is more or less corrugated, and may rest on a cushion formed by folds of the mucosa of the floor of the mouth. The degree of corrugation varies at different ages, for Anderson (1) showed that the tongue in the young *Platanista gangetica* is smooth, but its root is corrugated in the adult. In *Cephalorhynchus eutropia* a thick fold surrounds the tongue below the apex.

*Glands*:—The most marked features on the tongues of the Cetacea are the orifices of innumerable glands, and nearly every account records their presence. They vary greatly in extent and prominence, and they are more numerous than in all other Mammalia.

Genus *Orcella*:—In *O. fulminalis* many racemose glands open

into the basal limiting sulcus. In *O. brevirostris* there are no glands on the inferior surface, but the whole dorsum has patulous orifices. Those on the base of the tongue are very large.

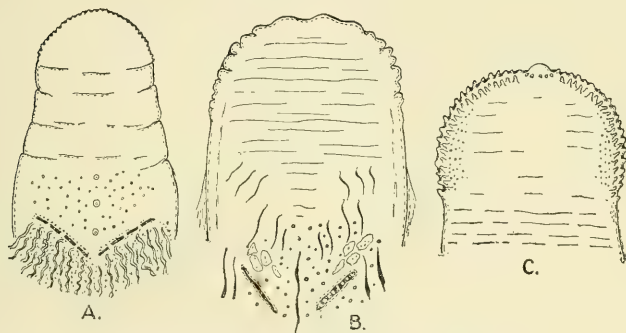
Genus *Platanista*:—The glands are numerous, but not as long as those in *Orcella*. Some open into sacs.

Genus *Mesoplodon* (text-fig. 28):—Numerous large and small glandular orifices are present, and there are five large sacs with linear orifices.

Genus *Lagenorhynchus* (text-fig. 26 B):—The orifices cover the posterior two-thirds of the tongue, and increase in size from before backwards. The central ones lie on elevations. No sacs are present, and there are no glands on the inferior surface.

Genus *Tursiops* (text-fig. 27 C):—Many small orifices surround the edges of the anterior part of the tongue, and there are large clusters beneath the tip.

Text-figure 27.



Tongues of the Cetacea. A: *Phocaena communis*; B: *Delphinapterus leucas*; C: *Tursiops tursio*.

Genus *Phocaena* (text-fig. 27 A):—No sacs are present, and many minute orifices crowd the posterior part of the dorsum.

Genus *Delphinus* (text-fig. 26 C):—Many small orifices, lying in the centre of small areas crowd the posterior part of the dorsum. And there are clusters of pores on each side of a median ventral elevation. Two sacs (s) are present on the base of the tongue.

Genus *Delphinapterus* (text-fig. 27 B):—No sacs are present, and the glands are restricted to the posterior part of the dorsum.

Genus *Cephalorhynchus* (text-fig. 25 B):—Innumerable small elevations with minute, but patulous, orifices cover the posterior part of the tongue and pharynx. No orifices are present on the inferior surface, and no sacs are present.

Genus *Physeter* (text-fig. 25 A):—The surface of the foetal tongue is pitted all over. But the nature of the specimen at

my disposal did not permit histological examination being made.

The lingual glands are tubular or branching, and vary in length. And authors who have described true vallate papillæ mention that glands open into the fossæ. Murie writes as follows of the tongue of *Globicephalus melas* (25): "It exhibits numerous glandular papillæ and depressions, probably the representatives of papillæ fungiformes; other larger and much deeper furrows behind may be circumvallate cavities or mucous glands."

Text-figure 28.



The tongue of *Mesoplodon bidens* showing glandular orifices and the five large sacs.

*Papillæ*:—In most Cetacea, papillæ are scanty or absent, and those which are present are usually tactile or mechanical in function. The sense of taste is very slight or absent, and in no other mammalian order is it so deficient.

Papillæ are most numerous in *Orcella* and *Platanista*. In the former the oral part of the tongue has filiform papillæ, and the pharyngeal part has pedunculated and sessile papillæ, arranged singly or in pairs at the mouths of large racemose glands. In the latter the free part is thick with filiform papillæ divided into processes.

*Grampus griseus* (text-fig. 26 A) has neither filiform nor fungiform papillæ. At the junction of the oral and pharyngeal parts of the tongue there are two rows of deep narrow slits in V-formation, but there is no mesial sulcus. Each row has six fissures. In the specimen in the Museum of the Royal College of Surgeons they are absent.

Owen (27) described four large fossulate papillæ in *Hyperoodon*. But Turner (34) recorded many crypt-like depressions and papillæ, and a vallate V in *Mesoplodon bidens*. In my specimen of *M. bidens* there are five large sacs, probably glandular in character.

In *Cephalorhynchus eutropia* (text-fig. 25 B) there are no filiform or fungiform papillæ. Between the oral and pharyngeal parts of the tongue are five fissures in V-formation.

In *Delphinus delphis* (text-fig. 26 C) the slits have closed lips. In *Delphinapterus leucas* (text-fig. 27 B) they are longer, and the lips of one are opened to disclose a row of globular bodies. *Phocena communis* (text-fig. 27 A) has eight small fissures placed end to end in V-formation.

Neither papillæ nor fissures are present in *Monodon monoceros*, *Lagenorhynchus albirostris* (text-fig. 26 B), *Delphinus phocena*, and *Balænoptera borealis*.

In no Cetacean is there any trace of lateral organs. It appears, therefore, that the gustatory function is practically absent.

The *Inferior Surface of the Tongue* is usually folded, both longitudinally and transversely, and its mucosa is usually soft all over. But there is a firm bounding zone in *Grampus griseus*, *Lagenorhynchus albirostris*, and *Physeter macrocephalus*. Some forms have glandular pits beneath the apex. In no case did I see any trace of a sublingua or plicæ fimbriatæ, but Schulte (29) described a small triangular sublingua in the foetal *Balænoptera borealis*.

The *frenum* is absent in *Delphinapterus leucas* and *Mesoplodon bidens*. It is slight in *Grampus griseus*, *Lagenorhynchus albirostris*, *Cephalorhynchus eutropia*, and *Phocena communis*. Schulte (29) said it is absent in the foetal *Balænoptera borealis*. Anderson (1) described it in the foetal *Orcella brevirostris*, but said it is absent in the adult. I observed a very marked frenum in the new-born *Physeter macrocephalus* (text-fig. 25 A). These observations would show that the Cetacea require a frenum while suckling, but not when they lead an independent existence.

No Cetacean has salivary papillæ or plicæ fimbriatæ.

### Summary.

1. The tongues of the Cetacea have their glandular organs better developed, but their gustatory and mobile functions are less, than in other Mammalia.



2. The tongues of the *Mystacoceti* agree with those of the *Odontoceti* as follows:—1. Filiform papillæ are scanty or absent. 2. The mucosa is more or less corrugated. 3. There is no trace of foramen cæcum, lytta, frenal lamella, lateral organs, and apical gland of Nuhn.

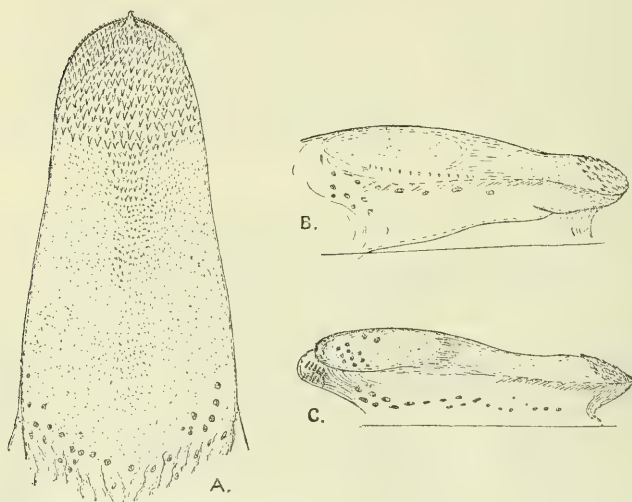
3. The tongues of the *Mystacoceti* and *Odontoceti* differ in the following points:—

<i>Mystacoceti.</i>	<i>Odontoceti.</i>
Tongue soft.	Tongue firm and hard.
Intermolar elevation present.	Absent.
Much oil in the tongue.	Absent.
Apex massive.	Not so.
Absent.	Marginal lobules present.
Lateral borders ill-defined.	Well-marked.
Glands less numerous.	Glands very numerous.
Muscles slight.	Muscles well-developed.
Mobility slight.	Mobility variable.

#### Order SIRENIA.

The tongues differ considerably from those of the *Cetacea*, and their characters approximate to those of the tongues of the *Ungulata*.

Text-figure 29.



Tongues of the Sirenia. A and B: dorsum and lateral aspect of the tongue of *Halicore indicus*; C: lateral view of the tongue of *Manatus americanus*.

The tongues (text-fig. 29) are firm and hard, but not very mobile. That of *Manatus* thickens progressively from before

backwards, but there is a distinct intermolar eminence. In *Halicore*, on the other hand, the posterior two-thirds are greatly elevated as in some Ungulata.

The *apex* is rounded and entire in both genera, and the *lateral borders* are entire and devoid of lobules which characterise the Cetacean tongue. Neither notches nor sulci are present.

The mucosa on the oral part is plain, but that on the pharyngeal part has many folds. The base has glandular openings arranged singly or in pairs. There are no glands on the inferior surface, and no apical gland of Nuhn is present. The glands are less developed than in the Cetacea.

*Papillæ*:—In both genera there is, behind the apex, a cluster of retroverted cuticular spines. And as the tongue is not very mobile they are of great assistance in cropping the vegetation on which the animals live. Behind that cluster the dorsum is plain in *Manatus*, but covered with a velvety pile of small papillæ in *Halicore*. Owen (27) figures a plain dorsum behind the spines in the latter.

In *Manatus*, according to Owen (27), there are many vallate papillæ. In *Halicore* they are represented by clusters of pits.

*Lateral Organs*:—In *Manatus* (4) these are well-developed and appear as large cushions with numerous fissures. In *Halicore* these are absent.

The *Inferior Surface* has many large orifices in *Manatus*, and many embedded cylindrical bodies in *Halicore*, but I was unable to examine the latter microscopically.

The *Frenum* is slight, and there is no frenal lamella, foramen cæcum, lytta, sublingua, or plicæ fimbriatæ. No comb-like structures are found on the infero-lateral aspect.

## Order UNGULATA.

### Suborders PERISSODACTYLA and ARTIODACTYLA.

In most species the tongue is long, comparatively narrow, and very mobile. But it is broad and flat in *Rhinoceros*. It has the greatest mechanical power in *Giraffa*.

The *apex* is truncated, pointed or rounded, and may or may not have a notch. In many species it has clusters of hard mechanical papillæ, as in the Sirenia. It is free in all forms, and this gives it considerable mobility.

The *lateral borders* are full and rounded. They may be comparatively smooth, or covered with prominent conical and fungiform papillæ. But *Sus* is the only genus with lateral lobules similar to those in the Cetacea.

The anterior part of the tongue is flat and very mobile. Posterior to that is an intermolar eminence which raises the food up to the molar teeth. Most posteriorly is a flat, thin, more or less glandular part.

The *intermolar elevation* is present in all families. It is entire

in all except the Rhinoceros in which it is cleft. And it is covered with papillæ belonging to one or more of the conical, fungiform, and vallate series.

In the Perissodactyla it is well-marked, but low and flat. It has only conical papillæ in *Equus caballus*. In *Tapirus indicus* it has both conical and fungiform papillæ. In *Rhinoceros* clusters of vallate papillæ cover its halves.

In the Suina it is also flat. And both conical and fungiform papillæ are present.

The Camelidæ have well-marked eminences. And they possess large vallate and very hard projecting conical papillæ in the Llama.

In the Cervidæ and Bovidæ the prominent eminence has very hard conical and fungiform papillæ, and the former vary considerably in size and shape. Clusters of vallate papillæ may invade the sides of the eminence. I did not examine a sufficiently large series of tongues to draw conclusions as to their value for purposes of classification.

The eminence is prominent in *Tragulus*, but flat in *Hyomoschus*.

When the posterior third of the tongue is examined it is seen how glandular orifices are numerous in the Perissodactyla, but few or absent in all other forms. And the characters of these structures in the different Mammalian orders, with special reference to the relation between their size and that of other parts of the oral glandular apparatus, have already been described.

It is seen in this paper that the Cetacea, which have no salivary glands, have large lingual glands; the Sirenia, which have small salivary glands, have fewer glands; and the Ungulata, with good salivary glands, have few lingual glands. Also the Perissodactyla have larger lingual glands than the Ruminantia.

*Circumvallate Papillæ* (text-fig. 30 A):—The number and arrangement vary, and the following patterns were observed by myself:—

1. No papillæ.
2. A pair of papillæ.
3. Several papillæ in a straight line, or wide-angled V.
4. Rows of papillæ on each side of the tongue.
5. Clusters or fields of papillæ.

In the Perissodactyla there are two large papillæ in *Equus caballus*, *E. asinus*, and *E. chapmanni*, but several observers noted three in *E. caballus*. Mayer (22) described a pair in *Tapirus americanus*, but I noted several in a straight line or wide-angled V in *T. americanus*, *T. indicus*, and *T. bairdi*. In *Rhinoceros* there is a field of ten papillæ on each side of the tongue.

In the Suina there is a pair of papillæ in *Sus scrofa*, *S. babirusa*, *Potamochoerus penicillatus*, *Phacochoerus aeliani*, and *Dicotyles torquatus*. Schwalbe (30) recorded three papillæ in *Sus scrofa*.

The Tylopoda have the largest vallate papillæ, and they are arranged in two converging lines on the narrow intermolar eminence. In *Camelus dromedarius* there are seven on each side in a single chain. But Mayer (22) stated that the seven in *C. bactrianus* are in two rows on each side—an inner one with three papillæ, and an outer one with four. In *Auchenia* the numbers of papillæ are not identical in each row.

The Tragulidæ have types of papillæ which are not found in any other group. There is a pair of long furrowed papillæ surrounded by a patulous fossa in both *Tragulus* and *Hyomys*; but Flower (14) described many small papillæ in the latter.

The tongue in *Giraffa* has more papillæ than that of any other mammal. Münch and Tuckerman counted fifty, and Owen (27) described two fields, each with 15–20 elements.

In the Cervidæ the papillæ are usually arranged in two rows on each side. And the following numbers were observed by myself, or recorded by others:—

<i>Muntiacus muntiac</i> .....	6	on each side.	
<i>Cervus elaphus</i> .....	26–28		(26).
,, <i>axis</i> .....	15–20	,,	,,
,, <i>dybowski</i> .....	20	,,	,,
,, <i>humilis</i> .....	10	,,	,,
<i>Capreolus caprea</i> .....	7–8	,,	,, (24).
<i>Rangifer tarandus</i> .....	5–6	,,	,, (22).
<i>Alces machlis</i> .....	18–20	,,	,, (33).
<i>Curiacus virginianus</i> .....	13	,,	,, (33).
,, <i>toltecus</i> .....	10–11	,,	,, (33).

In the Bovidæ there are rows of small papillæ on each side, and the number of rows are shown in the classification given below.

The following list contains the number of papillæ:—

<i>Bos taurus</i> .....	10–17	on each side.	
<i>Bison americanus</i> .....	18	,,	,,
,, <i>bonasus</i> .....	11	on one side, and 6 on the other	(33).
<i>Bibos indicus</i> .....	17–19	on each side	(33).
<i>Budorcas taxicolor</i> .....	14	,,	,, (36).
<i>Connocætes gnu</i> .....	20	,,	,, (36).
<i>Cephalophus maxwelli</i> .....	7	,,	,,
,, <i>dorsalis</i> .....	12	,,	,,
<i>Antilope mergens</i> .....	18–20	,,	,, (6).
<i>Rupicapra rupicapra</i> .....	10	,,	,, (19).
<i>Antilocapra americana</i> .....	36		(33).
<i>Capra hircus</i> .....	12	,,	,,
,, <i>ibex</i> .....	13	,,	,,
<i>Ovis aries</i> .....	12	,,	,,
<i>Ammotragus</i> .....	8	,,	,,

It is frequently difficult to determine by the naked eye whether a certain papilla is of the vallate or fungiform variety.

It appears, therefore, that the papillary patterns are distributed as follows :—

No papillæ .....	Hyracoidea.
A pair of papillæ .....	Equidæ, Suidæ, Phaco- cheridæ, Tragulidæ.
Papillæ in a line or V .....	Tapiridæ.
Papillæ in rows .....	Camelidæ, Cervidæ, and Bovidæ.
Papillæ in fields .....	Rhinocerotidæ and Giraffidæ.

The papillæ are oval, cylindrical, or conical with the bases of the cones projecting beyond the vallums. And the surface is smooth, granular, or lobulated (text-fig. 30 B.). The fossa is closed or patulous, and the vallum varies in prominence. Taste-buds are usually well-marked.

*Fungiform Papillæ* (text-fig. 30 C.E.F.):—The distribution on the dorsal and ventral surfaces varies in the different families. In appearance they are hemispherical, or almost pedunculated, and the surface is smooth, granular, or covered with processes. Many have rich supplies of taste-buds.

In the Perissodactyla they are not very numerous, but have the usual mammalian arrangement in clusters and rows; and those on the lateral borders are very numerous. In *Equus* there are none on the intermolar elevation, but there are prominent ones there in *Tapirus*. In neither genus is there a marked ventral papillary zone.

The tongues of the Suina have many papillæ on the dorsum, but few on the ventral surface. And those on the lateral borders may be very prominent.

In the Tylopoda the papillæ are not numerous on the dorsum, but they form a very wide ventral papillary zone. And in no other family is the latter so large.

In the Cervidæ there is a prominent cluster of papillæ behind the apex. Between it and the anterior extremity of the intermolar eminence there is an area possessing very few papillæ, but the latter is bounded laterally by papillary bands. The ventral papillæ are numerous, but small.

In the Bovidæ there is no thick apical, dorsal cluster, and the papillæ stretch right back from the apex to the intermolar eminence. They are only absent from a thin central strip of the dorsum. They are very regularly arranged. They are not numerous inferiorly in *Bison*, but they are numerous, small, and closely packed in *Antilope*, *Capra*, and *Ammotragus*.

In the Tragulidæ the papillæ are numerous on the dorsum, and have the usual arrangement. They are absent only from a narrow central strip.

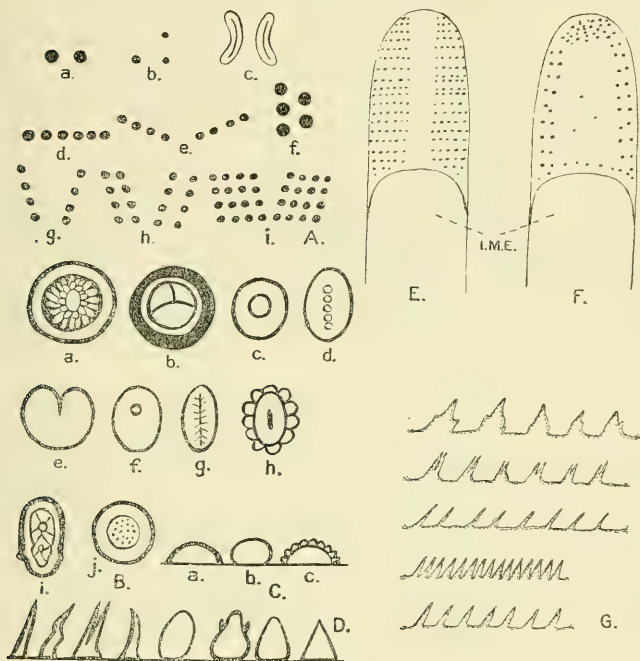


*Conical Papillæ*:—The teeth in the Ruminants are assisted by the action of the hard conical papillæ comminuting the food against the prominent palatal ridges.

In the Perissodactyla they are innumerable, slender, silky, and set very closely together. And their characters are similar over the entire dorsum.

In *Sus* the lateral borders of the tongue have innumerable long, club-shaped conical papillæ, as in the Cetacea. But no other genus of the Suina possesses them. In *Potamochaerus* the

Text-figure 30.



Tongues of the Ungulata. A (a-i): vallate papillary patterns; B (a-g): naked eye appearances of the vallate papillæ; C (a-c): fungiform papillæ; D: conical papillæ; E: fungiform papillæ of the Bovidæ; F: fungiform papillæ of the Cervidæ; I.M.E.: intermolar eminence; G: sublingual combs.

conical papillæ on the base are very large, pointed and directed backwards. In *Dicotyles* all the papillæ are very minute. The characters of the conical papillæ and lateral organs are useful for classifying the Suina (page 653).

In the Camelidæ the anterior part of the tongue has minute closely-set papillæ. But those on the intermolar elevation are large, flat, hard, and separated into two groups by a smooth central strip.

The Bovidæ and Cervidæ have papillæ similar to those in the Camelidæ, but those on the eminence are smaller, more numerous, and not divided into two groups.

In the Tragulidæ the conical papillæ on the dorsum are all small in *Tragulus*, but in *Hyomoschus* those on the base of the tongue are large, pointed, closely set, and directed backwards. Those on the base are not so disproportionately large in *Tragulus*.

The ventral papillary zone is narrow in the Perissodactyla, but wide in the Artiodactyla, especially the Tylopoda.

The conical papillæ are shown highly magnified in text-fig. 30 D.

*Lateral Organs*:—As Oppel (26) has collected the various published accounts, it is only necessary to show here their value for purposes of classification. They are frequently absent, and I would suggest that the lateral rows of circumvallate papillæ replace them in these cases.

In the Perissodactyla they are absent, according to Boulart and Pilliet (5), in *Tapirus americanus*, *Equus caballus*, and *Rhinoceros*. But they are well-marked in all the Tapiridæ examined by myself. Complete accounts of the organs have been published by Sertoli (32) and Hönigschmeid (19).

In the Suina they are present in *Sus*, *Phacochoerus*, and *Potamochoerus*, but they are absent in *Dicotyles*. The Babirusa has circular organs, but those in the other forms consist of rows of laminae and sulci.

In the remaining Artiodactyla they are present in the Giraffidæ, Tragulidæ, and *Antilope mergens*, but they are absent in all others examined.

The *Lytta* is represented by a median ventral ridge, which varies in width and prominence, but it is not at all like that in the Carnivora. And sections show that it has a central core.

In *Tapirus indicus* it is narrow, prominent, and firm. But it is wide, flat, and softer in *Equus*; and the structure in the latter has already been described by Brühl (7). Owen (27) recorded its presence in *Rhinoceros*. In all Perissodactyla it does not widen much from before backwards.

In *Dicotyles* it forms a long, narrow isosceles triangle.

The Tylopoda, as exemplified by the Llama, have short, prominent crests with very thick mucosa.

In the Tragulidæ it is broad and flat, especially in *Hyomoschus*. But it is most variable in the Cervidæ and Bovidæ. In these it is narrow and sharp, low and broad, or absent. The appearances, however, are of no value for purposes of classification.

On the infero-lateral aspects of the tongue there may be long bands with divided free edges, or rows of separate processes. They may help to keep the interstices between the teeth clear, or they may help to mix the food and saliva. They have not been named, so I suggest the term "sublingual combs" for them. They are restricted to the attached part of the inferior

surface of the tongue. The following arrangements have been observed:—

1. Combs absent—Perissodactyla, Suina, Hyracoidea.
2. Edges divided into triangles—Tylopoda, Tragulidæ.
3. Long, more or less separate processes—Bovidæ and Cervidæ.

Some forms are shown in text-fig. 30.

The *frenum* is always present, and permits the tongue to be very mobile. But there is no trace of a frenal lamella.

There is no trace of a foramen cæcum, sublingua or plicæ fimbriatæ, and the apical gland of Nuhn is present only in *Ovis aries*.

It has been the object of the above summary of the characters of the tongues of the Ungulata to show their value for purposes of classification. And they have been arranged schematically as follows. From that system it will be seen that the characters of the tongue are a useful addition to the external and skeletal characters at present in use.

*Classification.*—The following characters are valuable for purposes of classification:—1. Character of the orifices of glands on the base. 2. Nature of the intermolar eminence and its papillæ. 3. Arrangement of the vallate papillæ. 4. Lateral organs. 5. Sublingual combs. 6. Distribution of conical and fungiform papillæ.

#### Suborder PERISSODACTYLA.

Numerous orifices of glands on base. No combs. Conical papillæ silky and closely-set. Ventral papillary zone very small or absent.

- |                                                                                                      |                    |
|------------------------------------------------------------------------------------------------------|--------------------|
| A. Intermolar eminence cleft. Vallate papillæ in fields. No lateral organs .....                     | <i>Rhinoceros.</i> |
| B. Eminence low, flat, and entire.                                                                   |                    |
| <i>a.</i> A pair of vallate papillæ. No lateral organs. No fungiform papillæ on eminence .....       | <i>Equus.</i>      |
| <i>b.</i> Vallate papillæ form a row or V. Lateral organs present. Large fungiforms on eminence..... | <i>Tapirus.</i>    |

#### Suborder ARTIODACTYLA.

Few or no orifices of glands on base. Combs variable. Conical papillæ hard and not so closely set. Ventral papillary zone well-marked.

- |                                                    |                       |
|----------------------------------------------------|-----------------------|
| A. No sublingual combs. Two vallate papillæ.       |                       |
| <i>a.</i> Edges of tongue have long processes..... | <i>Sus.</i>           |
| <i>b.</i> No long processes present.               |                       |
| <i>i.</i> Papillæ on base immense .....            | <i>Potamochoærus.</i> |
| <i>ii.</i> Papillæ on base not immense.            |                       |
| <i>a'.</i> Lateral organs present .....            | <i>Phacochoærus.</i>  |
| <i>b'.</i> No lateral organs .....                 | <i>Dicotyles.</i>     |

## B. Sublingual combs present.

- a. A pair of long, narrow vallate papillæ.
  - i. Basal conical papillæ small..... *Tragulæ.*
  - ii. Basal conical papillæ very large ..... *Hyomochus.*
- b. A single row of immense vallate papillæ on each side... *Camelus, Auchenia.*
- c. One or more rows of small vallate papillæ on each side.
  - i. Fungiform papillæ absent from an extensive area in front of the intermolar eminence. Two rows of vallate papillæ ..... CERVIDÆ.
  - ii. Fungiform papillæ stretch right back to eminence, but are absent from a central strip on the anterior part of the dorsum.
    - a'. One row of vallate papillæ on each side ..... *Cephalophus.*
    - b'. Two rows on each side ..... *Bos, Ovibos, Bison, Camochates, Strepsiceros, Antelope.*
    - c'. Four rows on each side ..... *Budorcas, Ovis.*

## Suborder HYRACOIDEA.

The tongue in *Hyrax* has a low, flat elevation similar to that in *Halicore*, and the lateral organs are well-marked. There is no vallate papilla in several specimens examined by myself, and by Brücher (6), Gmelin (16), Munch (24), and Tuckerman (33). And there is no trace of a lytta. All conical papillæ are minute. The basal lingual glands have few orifices on the surface. It is evident, therefore, that the tongue has some affinities with those of the Sirenia. No sublingual combs are present.

## Suborder PROBOSCIDEA.

The tongue is short and wide, and it corresponds to the intermolar elevation of the other Ungulata. The apex is bound down to the floor of the mouth, as in the Cetacea. In *E. indicus* Mayer (22) observed six papillæ, but Miall and Greenwood (23) recorded four. In the specimen examined by myself there were two on the right side and one on the left. In *E. africanus* Forbes (15) saw four papillæ on the right side, and three on the left, but Münch (24) observed three on each side. The lateral organs are well-developed, but their contained taste-buds are sometimes very few. No sublingual combs are present.

## SUMMARY AND CONCLUSIONS.

1. The Cetacea have simpler tongues than any other mammals.
2. The tongues do not support the view of some authorities that there are affinities between the Cetacea and Ungulata. But the differences between them are due to the nature of the diet and the mode of feeding. And the nature of the food causes the Sirenian tongues to resemble those of the Ungulata in some points.

The essential differences between the Cetacea, Sirenia, Artiodactyla, and Perissodactyla are :—

*Cetacea*—Mobility slight. No gustatory organs. Glands numerous. An intermolar eminence is only present in some Mystacoceti. Few or no mechanical papillæ.

*Sirenia*—Mobility greater. Slight gustatory organs. Glands fewer. Small intermolar eminence. Mechanical papillæ present.

*Artiodactyla and Perissodactyla*—Mobility great. Well-marked gustatory organs. Glands variable, being numerous in the latter and few in the former. Intermolar eminence well-marked, but variable in size. Mechanical papillæ well-marked.

3. The characters of the tongue have several points in common in the Artiodactyla and Perissodactyla, but those of the Hyracoidea and Proboscidea are such as to separate them into groups by themselves. Of these the Hyracoidea have some resemblance to the Sirenia.

4. The Cetacea are the only mammals in which the tongues may lie far back in the mouth.

5. The tongues of the Mystacoceti differ from those of the Odontoceti.

6. The tongues of the Mystacoceti contain large quantities of oil, but this is absent in all other mammals.

7. The excessive development of cuticular spines on the anterior part of the tongue in the Sirenia allows great use to be made of the moderate mobility.

8. The Perissodactyla differ from the Artiodactyla in the characters of the glands on the base of the tongue.

9. Sublingual combs are only present in the Camelidæ, Tragulidæ, Cervidæ, and Bovidæ.

10. It is impossible to distinguish the genera of the Cervidæ from one another by the characters of the tongue.

11. The distribution of the fungiform papillæ is a good means of telling the Cervidæ from the Bovidæ.

12. The Hyrax and Cetacea are the only mammals in which I was unable to detect vallate papillæ.

13. The sheep (*Ovis aries*) is the only mammal below the Primates which possesses the apical gland of Nuhn.

14. The characters of the fungiform papillæ distinguish the deer from the antelopes.

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34. The External Characters of *Scarturus* and other Jerboas, compared with those of *Zapus* and *Pedetes*. By R. I. Pocock, F.R.S., F.Z.S.

[Received May 9, 1922: Read May 23, 1922.]

(Text-figures 29-37.)

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#### INTRODUCTION.

At the Scientific Meeting of the Zoological Society held on May 24th of last year (P.Z.S. 1921, p. 645), Major Flower exhibited examples of three species of Egyptian Jerboas (*Jaculidæ*), including a pair of the very rare four-toed form, *Scarturus tetradactylus*, which had never been previously imported to Europe alive, and was almost unknown in museums, apart from the original example in Berlin, which was described as *Dipus tetradactylus* by Lichtenstein in 1823. These examples were exhibited in the Zoological Gardens for some months, but died in the winter and came into my hands for examination\*. To compare with them I had several specimens of the two common Egyptian Jerboas (*Jaculus jaculus* and *Scirtopoda orientalis*)†; and also one of the five-toed genus *Allactaga* (*A. indica*), a pair of examples of *Zapus hudsonianus* or a nearly related species, and one male specimen of *Pedetes caffer*—the last-mentioned examples having been preserved for many years in alcohol in the Society's collection. The specimens above mentioned form the material upon which this paper is principally based.

\* Although apparently fully adult when received, all the skeletal tissues at the time of death were exceedingly frail. Even the tips of the incisor teeth were uncalcified and pliable—a condition I never before observed in any mammal.

† Good figures, drawn from life, and descriptions of these, as well as a brief account of *S. tetradactylus*, may be found in Anderson and de Winton's 'Mammalia of Egypt.' My reasons for adopting the name *Scirtopoda* are given below (p. 679).

That *Zapus* belongs to the same group of Rodents as *Jaculus* has long been admitted, and is disputed, so far as I am aware, by no one acquainted with this order. The evidence rests mainly upon certain cranial characters connected more particularly with the zygomatic arch and the preorbital foramen, the structure of which distinguishes that genus from the Muridæ, despite the generally murine shape of the skull. It is also conceded that *Sicista*, formerly known as *Sminthus*, is tolerably closely related to *Zapus*. With regard to *Pedetes*, my pretext for including that genus in this paper is its former ascription to the same section\* as *Zapus* and *Jaculus*, although now recognised as representing a quite distinct family, sometimes associated with the Hystricomorpha, together with the family Anomaluridæ.

### *External Appearance.*

The general appearance of *Sicista* and *Zapus* may be described as murine. They have a long mouse-shaped head and comparatively small diurnal eyes, and, although the hind legs of *Zapus* are elongated and saltatorial, they are not very much longer relatively than in our common wood-mouse, *Apodemus sylvaticus*. The Jerboas, on the other hand, are not the least like typical murine rodents in appearance. The head is very large, wide, and, as a rule, short especially in the snout, which is deep from above downwards, and the eyes are relatively enormous and nocturnal. The hind legs are of great length and the fore limbs are short. A Jerboa with the fore limb, measured from the elbow, of approximately the same length as that of a *Zapus* has the foot, measured from the heel, about twice as long as that of *Zapus*. Hence, when progressing on all fours, the gait of a Jerboa is exceedingly awkward, owing to the great elevation of the hind quarters. They seldom adopt that mode of progression, usually employing their hind legs alone. When moving at speed they take prodigious hops, like a Kangaroo; but they frequently go at a more leisurely pace, trotting or striding along like an ostrich or a human being, an action of which Kangaroos, and, presumably, *Zapus* also, are quite incapable.

The great variation in the size of the ears affects the appearance of different species of Jerboas when compared with one another. They also differ in the shape of the muzzle. As above stated, the muzzle is typically short and truncated; but in *Euchoreutes*, hence named *naso*, it is relatively long. Presumably also *Allactaga*, although I have never seen a living example, must have a differently shaped muzzle from *Jaculus* on account of the prominence of the upper incisor teeth, which form an angle instead of, as in *Jaculus*, a continuous curve with the nose. *Scarturus* is intermediate between the two genera just mentioned with respect to the direction of these teeth.

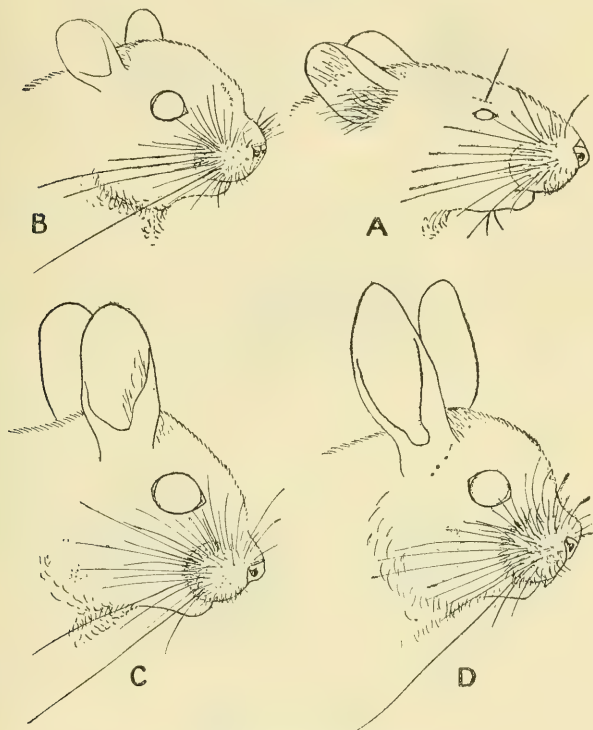
\* See Flower and Lydekker's 'Mammals, Living and Extinct,' p. 480 (1891).



*The Rhinarium and Mouth.*

In *Zapus* the rhinarium is well defined and marked by a distinct vertical groove, formed by the thickened bulging upper and inner margin of the nostrils. Above the thickening of the upper rim there is a short transverse area. The area below the rhinarium, extending from the nostrils to the edge of the

Text-figure 29.



- A. Head of *Zapus hudsonianus*.  
 B. „ *Jaculus jaculus*.  
 C. „ *Scirtopoda orientalis*.  
 D. „ *Scarturus tetradactylus*.

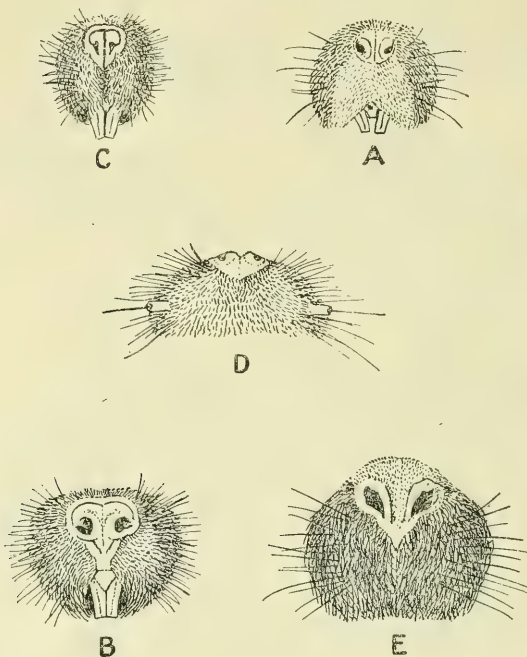
upper lip, is covered with shorter hair than the rest of the muzzle. There is no sign of a groove or philtrum dividing the upper lip in the middle line. (Text-fig. 30, A.)

From Miller's description of the rhinarium of *Sicista loriger* (Cat. Mamm. Western Europe, p. 537, 1912), it seems that the muzzle resembles in general features, at all events, that of *Zapus*,

He describes the anterior border of the nostril as thickened, with a small wart beneath it [? the nostril], and the space between the nostrils as narrow, marked by a well-developed vertical ridge, and the upper lip as having no groove in front.

In *Jaculus*, *Scirtopoda*, and *Scarturus* the rhinarium is very like that of *Zapus*, showing a similar thickening of the upper and inner rim and a median groove, but the area below the rhinarium

Text-figure 30.



- A. Muzzle and rhinarium of *Zapus hudsonianus*.
- B. " " " *Scirtopoda orientalis*.
- C. The same, contracted.
- D. Muzzle and rhinarium of *Jaculus jaculus*, to show especially the papillæ, slightly enlarged and cleared of hair, carrying the long stout vibrissæ.
- E. Muzzle and rhinarium of *Pedetes caffer*.

in the middle line is naked and constitutes a kind of shallow philtrum. Of the muzzle of this genus, Anderson and de Winton said:—"Over the bare area of the nose of *Jaculus* there is a thickened fold of skin capable of being drawn forwards, so as almost to cover the nostrils, this structure serving to protect them when the animal is using its broad snout to push out the earth

when digging its burrow" (Mamm. Egypt, p. 304). The rhinarium when thus partially concealed also contracts very perceptibly, the nostrils are approximated and assume a more vertical appearance, and the philtrum is obliterated by the median juxtaposition of the two halves of the upper lip. This device probably serves to exclude fine blown sand, as well as the soil when digging is in operation. (Text-fig. 30, B, C.)

The rhinarium of *Pedetes* is quite unlike that of *Zapus* and *Jaculus*. It is covered above and in front with fine short hair; but the nostrils, which are elongated and appear to be valvular, are surrounded by a narrow rim of naked skin. The median portion of the rhinarium below the nostrils in front is angled, but there is no trace of groove or philtrum dividing the deep upper lip, which is covered uniformly with longish hair (text-fig. 30, E).

Both in *Zapus*, *Jaculus*, *Scirtopoda*, and *Scarturus*, the mouth is provided with well-developed palatal and lingual lobes jutting inwards from the cheek. The palatal lobes meet along the middle line of the palate, but are separable and do not fuse in the middle line, the epithelium of the palate being smooth. The lingual lobes, which are long, meet in the middle line over or in front of the tongue, forming a secondary floor to the mouth. *Zapus* is provided with cheek-pouches opening just inside the corner of the mouth. The *Jaculidæ* are without them, and, so far as I am aware, they have never been recorded in *Sicista*.

In connection with the mouth, reference may be made to the presence in some genera of grooves on the incisor teeth. Their incidence is remarkable and puzzling. They are absent in *Sicista*, the least specialised genus of the group; but are present in *Zapus*, which seems to be much more nearly akin to *Sicista* than it is to any genus of *Jaculidæ*. Within the *Jaculidæ*, the grooves are present in *Dipus*, *Jaculus*, *Scirtopoda*, and *Cardiocranius*; absent in *Allactaga*, *Scarturus*, *Euchoreutes*, and *Pygeretmus*. Their presence, as recorded by Satunin, in *Cardiocranius*—a genus resembling *Pygeretmus* in possessing five toes on the foot and a specialised broad lanceolate tail—suggests that the character has no great systematic value.

#### *Facial Vibrissæ.*

The mystacial vibrissæ are well developed in *Zapus*. One or two long superciliary vibrissæ are also present; but in the long hairs clothing the cheek I failed to find the genal tuft. The interramal is represented by two very fine vibrissæ in one example. In the *Jaculidæ* the interramal tuft is apparently absent, and the superciliaries and genal tufts are of inconstant occurrence, and represented at most by one or two fine vibrissæ each. But the mystacials are well developed, one of them on each side set low down being stouter and longer than the rest. This

peculiarity is not so well marked in *Allactaga* and *Scarturus* as in *Jaculus*; but the two common Egyptian Jerboas differ somewhat in this respect. In *Scirtopoda orientalis* this long bristle is distinctly stouter and stiffer than the rest, and rises from a small papillary root, whereas in *J. jaculus* the difference is considerably greater, and the papilla from which it arises is much larger. (Text-fig. 30, D.)

In *Pedetes* the mystacial vibrissæ are comparatively few in number and short, although stout. A few longish superciliaries are present. The interramal tuft is apparently absent; but the genal is represented by two or three long vibrissæ set high up the cheek a little behind and below the posterior angle of the eye as in the *Hystricomorpha*.

By the characters mentioned above the genera may be arranged as follows:—

- a. Rhinarium ill defined, covered with hair except immediately round the nostrils, which are not visibly swollen and have no median groove between them; superciliary and genal vibrissæ well developed; mystacials stout and comparatively short ..... *Pedetes*.
- a'. Rhinarium well defined, naked, nostrils with swollen rim and a groove between them; superciliary and genal vibrissæ few or absent, mystacials long and slender for the most part.
- b. Head narrow and low, murine in shape; no median groove on upper lip; mouth with cheek-pouches (? in *Sicista*) ..... *Zapus*, *Sicista*.
- b'. Head broad and high; upper lip divided by philtrum, no cheek-pouches ..... *Jaculus*, *Scirtopoda*, *Scarturus*\*.

### *The Ear.*

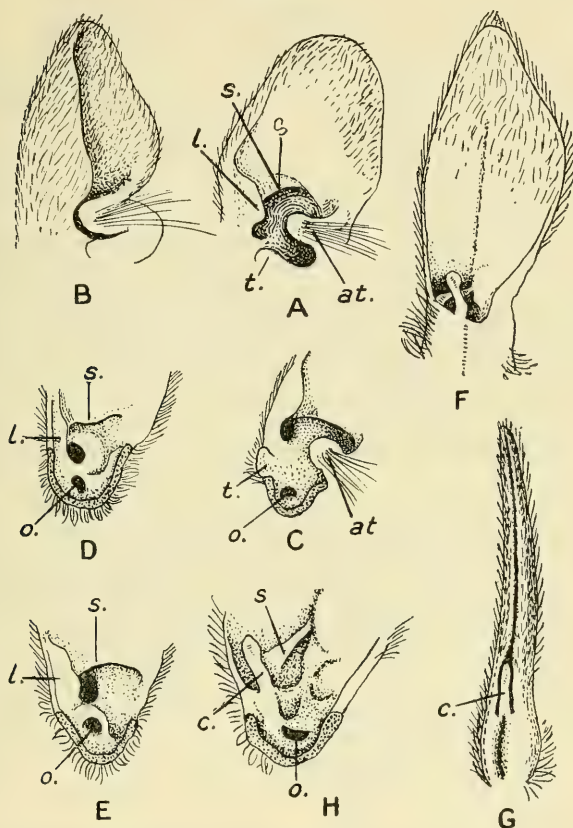
In *Zapus* the ear is moderately large and expanded, and arises from the head by a broad base which is not tubular. The anterior edge is normally overfolded, and inferiorly about on a level with the supratragus it is produced into a lamina which is normally folded inwards out of sight. The lower edge of this curves into the cavity of the ear and ceases on its floor. The tragus is represented by a small movable lobe, and the antitragus by a large tufted lamina which, when the ear is folded, projects forwards and closes the lower portion of the cavity. The orifice is situated just below and on the inner side of the deep intertragal notch. (Text-fig. 31, A-C.)

Miller describes the ear of *Sicista loriger* as "moderately large, extending a little beyond the eye when laid forward, its outline simple, ovate, its posterior border with large thickened lobe at base, capable of completely closing the meatus, its anterior border with minute though evident sub-basal notch and projection; both surfaces of ear densely clothed with short hairs; basal lobe conspicuously tufted." This description might have been taken

\* I have not seen a sufficient number of specimens of *Allactaga* and other Asiatic genera of *Jaculidæ* to know whether the cleavage of the upper lip is a constant character in this group or not.

from the ear of *Zapus*, with the anterior flap concealed, as is normally the case, by being folded inwards.

Text-figure 31.



A. Ear of *Zapus hudsonianus*, expanded.

B. The same, contracted.

C. Base of ear of the same, with basal portion cut open between tragus and antitragus.

D. The same of *Scirturus tetradactylus*.

E. The same of *Scirtopoda orientalis*.

F. Expanded ear of *Pedetes caffer*.

G. Folded ear of the same.

H. Base of the ear of the same, cut open.

*l.*, infolded lamina of anterior border; *t.*, tragus; *at.*, antitragus; *s.*, supratragus; *o.*, orifice of ear; *c.*, columnar process.

In the *Jaculidae* the ears vary greatly in length. In *Euchoreutes*, the longest-eared form, they considerably overlap the tip of the exceptionally long snout, when turned forwards. In



*Scarturus*, which has a short snout, they surpass it by a little. In *Allactaga indica* they reach about to the end of the muzzle, and in most species assigned to this genus they appear, judging from Lichtenstein's figures, to reach well beyond the eyes at all events. In *Scirtopoda orientalis* they overlap the eyes by a little; in *J. jaculus* they just cover them. In other species figured by Lichtenstein they are as short as in the typical species or shorter. But despite their length they all appear to be similarly constructed. They are more or less tubular at the base, the orifice being sunk deep down within the cavity. There is no trace of tragal lobe or antitragal flap, such as are seen in *Zapus* and *Sicista*; but just within the anterior edge, on a level with the supratragus, there is a delicate membranous lamina descending, as in *Zapus*, into the tubular basal portion and normally folded in out of sight. The lower end of this lamina curves backwards and inwards, and just inside its lower end there is a deep cavity bounded above by the anterior end of the supratragus, which is a slender delicate ridge running backwards towards the posterior edge of the ear, exactly as in *Zapus*. The orifice is situated a little below this anterior cavity, and is separated from it by a thickening. There are minor differences in the structure of the ear which may prove to have systematic importance, but my material is not sufficient in quantity to establish the point. In *Scirtopoda orientalis*, for instance, the anterior infolded lamina is larger than in *Scarturus*, and the area round the auditory orifice is more swollen. In *Scarturus*, on the other hand, the lower end of the passage leading to the anterior pit is much more swollen than in *S. orientalis*, and the tubular portion of the ear is provided with a fine delicate lamina ascending from a point behind the auditory orifice up to the position of the aborted antitragus. This is not so noticeable in *S. orientalis*. Selater's brief description of the ear of *Euchoreutes* contains nothing to suggest any difference between that genus and the three I have examined in the structure of the organ in question. (Text-fig. 31, D, E.)

From what has been said above it will be clear that the kinship claimed to exist between *Zapus* and the Jaculidæ on cranial grounds is completely borne out by the ear. The ear of the Jaculidæ may be regarded as a derivative of the type seen in *Zapus*, specialised by its more tubular base, with which the disappearance of the tragus and antitragus is correlated. In the Jaculidæ, too, the anterior basal pit is deeper and its inferior edge is closer to the auditory orifice.

The ear of *Pedetes* is very different from those described above, although in its tubular base and its length it recalls in appearance the ear of some Jaculidæ. It shows, however, in its posterior border behind the tip, a shallow but long emargination, similar to the emargination so common in many of the Hystricomorpha. The anterior edge is not overfolded and there is no inturned lamina at the base. There is no antitragus, but from the inner side of

the outer wall of the tubular base there arises a compressed process which projects upwards as a free outgrowth some little distance above the margin of the basal tubular portion. When the ear is expanded this process, which possibly represents the tragus, inclines forwards along the edge of the ear in front of it. The supratragus is a well-defined ridge running upwards and backwards, but stopping abruptly in the middle of the ear far away from its posterior edge; and the wall of the ear between the posterior end of the supratragus above and the auditory orifice below is folded and creased. (Text-fig. 31, F-H.)

The reason for the termination of the supratragus in the middle of the ear is this. When the ear is folded, it doubles up exactly lengthwise along the middle line, so that the anterior and posterior margins are evenly in contact throughout their length, except close to the basal tubular portion; but the space that is left between them at this spot is filled by the process above described, and that appears to be its function. The grooving of the wall of the lower portion of the ear is also subservient to this peculiar method of folding, which could not be effected if the rigid supratragus extended across the cavity of the pinna.

By the structure of the ear the genera discussed fall into the following three headings:—

- a. Ear long, folding exactly along the middle line, so that its anterior and posterior edges coincide; a columnar process rising from its basal tubular portion; supratragus a well-defined thickened ridge. No intumed flap at the base of the anterior edge in front ..... *Pedetes*.
- a'. Ear long or comparatively short, not folding so that the two edges of the pinna exactly coincide; no columnar process rising from its basal portion; a distinct intumed flap at the base of the anterior edge in front. Supratragus comparatively weak.
- b. A small tragus and large antitragus, base of pinna not tubular. *Zapus, Sicista*.
- b'. No tragus or antitragus; base of ear more or less tubular. *Jaculus, Scirtopoda, Scarturus, Allactaga*.

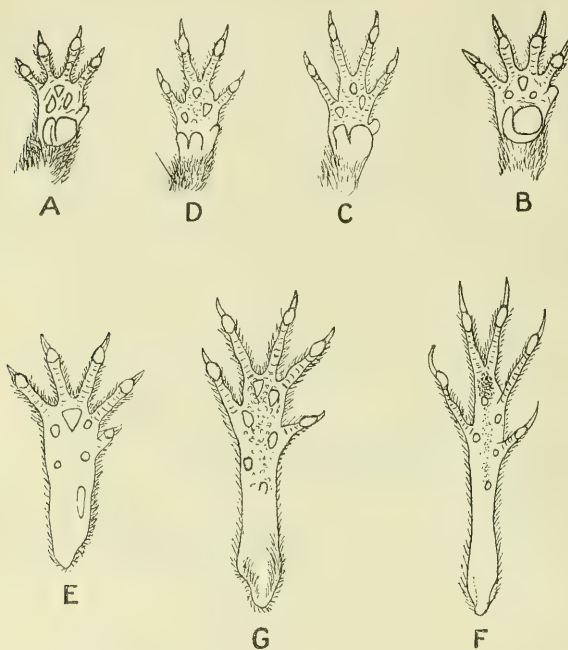
### *The Fore Foot*

In *Sicista subtilis*, judging from Tullberg's figure, the fore foot is comparatively broad, short, and unmodified; the four main digits are subequal in length, the third and fourth projecting a little beyond the second and fifth, the latter being a little shorter than the second; the first, or pollex, is quite short, and springs from the middle of the side of the foot close to the distal edge of the carpal pad. The digital pads are moderate in size and elliptical, and the claws are small. The plantar pad consists of three moderately large interdigital elements, subtriangular in shape and in contact or nearly so. The carpal pads are large, covering about half the area of the sole, the internal element being about twice the area of the external, which is in contact with it. (Text-fig. 32, B.)

The fore foot of *Zapus* is comparatively long and narrow. The carpal pads and pollex are tolerably similar to those of *Sicista*,

but the three interdigital elements of the plantar pad are small, obscurely defined, circular tubercles widely separated from each other. The four main digits, moreover, are longer and thinner than in *Sicista* and unevenly spaced, the third and fourth being close together at the base, but the second is some distance from the third, and the fifth from the fourth. The claws are comparatively long, and the sole of the foot is granular. The foot is a slight exaggeration of the type seen in *Apodemus sylvaticus*, the common

Text-figure 32.



- A. Right fore foot of *Scarturus tetradactylus*.  
 B. The same of *Sicista subtilis* (after Tullberg).  
 C. The same of *Zapus hudsonianus*.  
 D. The same of *Apodemus sylvaticus*, for comparison with C.  
 E. Right hind foot of *Sicista subtilis* (after Tullberg).  
 F. The same of *Zapus hudsonianus*.  
 G. The same of *Apodemus sylvaticus*, for comparison with F.

English wood-mouse, the third and fourth digits being conjointly a little more removed from the second and fifth. (Text-fig. 32, C.)

The fore feet of the Jerboas (*Jaculidæ*) seem to resemble very closely those of *Sicista* in a general way, except that the claws are much longer, being generally very long, and the interdigital elements of the plantar pad greatly reduced in size. In *Scarturus* they are represented by three widely separated circular papillæ ;

in *Euchoreutes*, according to Sclater, there are only two, corresponding apparently to the median and outer of *Scarturus*; in *Allactaga indica* I can find only the median remaining, whereas in *Scirtopoda orientalis* and *J. jaculus* all definite trace of them seems to have disappeared, the sole of the foot in front of the carpal pads being merely marked by integumental creases. As in *Sicista* and *Zapus*, the carpal pad is double, the outer or ulnar element being comparatively small, while the inner or radial is very large, especially in *Allactaga indica*, where it occupies practically the whole of the posterior half of the sole. The pollex is a mobile cylindrical process, covered above with a large nail in *Jaculus*, *Scirtopoda*, *Scarturus*, and *Allactaga*, but in *Euchoreutes*, according to Sclater, it is armed, like the other digits, with a long claw. This author also described the digits of *Euchoreutes* as long, but, judging from the figure, they are no longer than in other genera of *Jaculidæ*. As in several Rodents, notably the Squirrels, objects are held in the fore foot by folding the four digits back upon the large carpal pad, which plays the part, as it were, of a thumb. (Text-fig. 32, A.)

The fore foot of *Pedetes* is short and broad, and has five well-developed digits, all armed with long, stout, nearly straight claws—the pollex being like the others, but shorter. The digital pads are scarcely defined; and the under sides of the digits and the short area of the sole distal to the carpal pads are naked and granularly roughened. No trace of plantar pads remains. The carpal pads are remarkable and, so far as I know, unique. They are very large. The inner pad is an elevated thickened cushion, beset on the summit with minute spicules. The inner pad is laminate and normally fits closely against the outer pad, but is independently movable like a valve, so that a deep space separates the summits of the two pads. Its free edge, moreover, bears a fringe of long hairs. This modification suggests that the carpal pads are prehensile and aid in the grasping of food that is gripped by the digits with their long claws. These claws are no doubt also fossorial. (Text-fig. 35, A-C.)

From the following summary of the characters of the fore foot it will be seen that *Pedetes* stands apart from the other genera. It may be noted, however, that *Sicista* falls with the Jerboas and not with *Zapus* :—

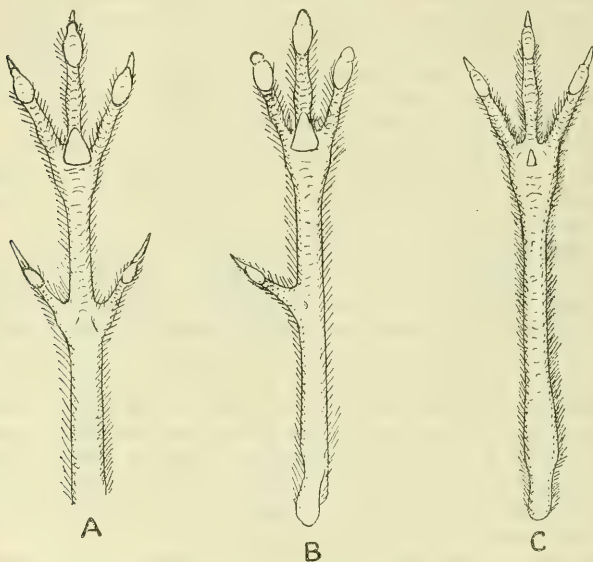
- |                                                                                                                                                                                                                             |                                                            |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------|
| a. Fore foot with well-developed pollex armed with a claw as long as on the other digits; claws very long, stout, and straight; carpal pads separable and prehensile, the movable outer pad with fringe of long hairs ..... | <i>Pedetes.</i>                                            |
| a'. Fore foot with short pollex armed with a nail or slender claw; claws of digits 2 to 5 long or short, but slender and curved; carpal pads normal, confluent, the outer immovable and not fringed.                        |                                                            |
| b. Foot elongated and narrow, digits unevenly spaced, 3 and 4 in advance of 2 and 5 .....                                                                                                                                   | <i>Zapus.</i>                                              |
| b'. Foot short and broad, digits 2 to 5 evenly spaced.                                                                                                                                                                      |                                                            |
| c. Pollex armed with small claw (sec. Sclater) .....                                                                                                                                                                        | <i>Euchoreutes.</i>                                        |
| c'. Pollex armed with broad blunt nail .....                                                                                                                                                                                | <i>Sicista, Jaculus, Scarturus, Scirtopoda, Allactaga.</i> |



*The Hind Foot.*

The hind foot in *Sicista subtilis*, according to Tullberg's figure, is much broader and shorter than in *Apodemus sylvaticus*, but closely resembles in those particulars the foot of *Rattus norvegicus*. The hallux is shorter than in that species and closer to the second digit, and the second, third, fourth, and fifth digits are subequally spaced and close together, as in the fore foot, the third and fourth projecting a little beyond the second and fifth. The claws are short and the digital pads normal and semi-elliptical. The plantar pad is represented by four separated interdigital elements, the median being comparatively large and

Text-figure 33.



A. Right hind foot of *Allactaga indica*.

B. The same of *Scarturus tetradactylus*.

C. The same of *Jaculus jaculus*, with hair cut short.

triangular, the others much smaller and subcircular, the one at the base of the hallux being remote from the rest and only a little in advance of the external metatarsal pad, which is also quite small and subcircular, while the internal metatarsal pad is elongated and situated near the inner edge of the foot halfway between the heel and the hallucal element of the plantar pad. (Text-fig. 32, E.)

The hind foot of *Zapus* is very different from that of *Sicista*. It is very long and slender, the second, third, and fourth digits being well in advance of the first and fifth, with the second



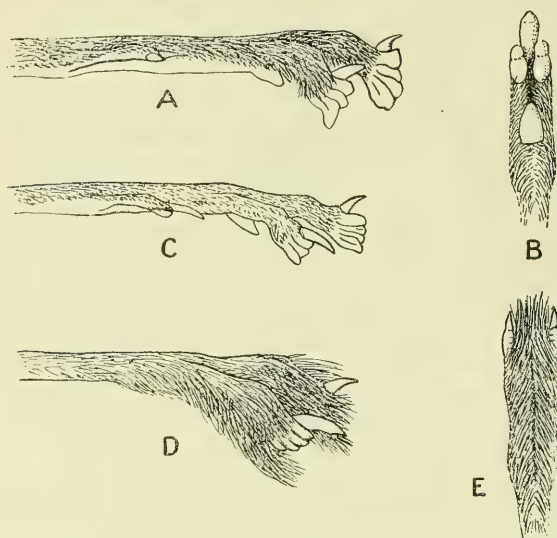
farther from the third than the latter is from the fourth, these two being closely united proximally. The hallux is moderately long and slender, and rises a little behind the origin of the fifth; it reaches to the base of the second, which is shorter than the third approximately by its digital pad; the fifth reaching only to the distal end of the narrow webbing tying the third and fourth closely together proximally. The claws are long and slender, and the digital pads elliptical. The plantar pad is represented by four small, isolated, subcircular, interdigital elements set on the granular sole in accordance with the disposition of the digits. The metatarsal pads are represented merely by the internal element, which is a small subcircular pad set one-third of the distance along the metatarsal area between the hallux and the heel. (Text-fig. 32, F.)

The hind feet of the *Jaculidæ* differ profoundly from those of *Zapus* in the disposition of the digits and other particulars. They are markedly perissodactyle, the third digit being the longest, set in the middle line, and symmetrically flanked on each side by the second and fourth, which are equal in length and rise at the same level. Their digital pads are moderately or very large, deep, compressed, and laterally grooved, with lobulate distal edge. The plantar pad is represented by a larger or smaller soft median papilla, pointed apically. The metatarsus is much longer than in *Zapus*, and, as is well known, the three bones corresponding to the three main digits are completely fused into one. The first and fifth digits may be absent or present. When present they rise a long way back on the metatarsus, and, since they do not normally touch the ground, have been described as functionless. They are slender, with a small normal digital pad and thin longish claw. The metatarsal bone proper to each remains distinct from the median "cannon" bone, and, when both these digits are retained, they spring from the side of the metatarsus at the same level. Progressive reduction in the number of digits from five to three is shown in the family. In *Pygeretmus*, *Allactaga*, and *Euchoreutes* the first and fifth are retained. In *Scarturus* the first is lost and the fifth retained. In *Jaculus* both are lost. The under side of the digits varies greatly in hairiness. In the two Egyptian species, *Jaculus jaculus* and *Scirtopoda orientalis*, they are thickly fringed on each side with long hairs, which curve inwards over the under surface of the digits and form a soft hairy cushion. Close to the pads these hairs are exceptionally long. They quite conceal the median pad from the lateral aspect, but the pads of the second and fourth digits are not entirely covered by them. In these two hairy-footed species the median plantar papilla is very small and soft, and the digital pads are comparatively small. In *Scarturus*, which occurs in the same localities as *Scirtopoda orientalis*, on the contrary, the under sides of the digits have no long fringes, and the digital pads are very large and deep, and more strongly grooved and marginally lobate than in *Scirtopoda orientalis* and

*Jaculus jaculus*. They conceal the claws from the lower aspect of the foot, but these claws are smaller than in *J. jaculus* and *S. orientalis*. The plantar papilla, moreover, is a large conical eminence. The three main digits of *Allactaga indica* resemble those of *Scarturus tetradactylus* in the comparatively scanty development of hairs on the under side; but the pads do not appear to be so large\*. Nevertheless, the plantar papilla is a large conical eminence as in *Scarturus*. (Text-figs. 33, 34.)

In the four species of this group above described the claw of the median digit is considerably smaller than those of the lateral digits.

Text-figure 34.



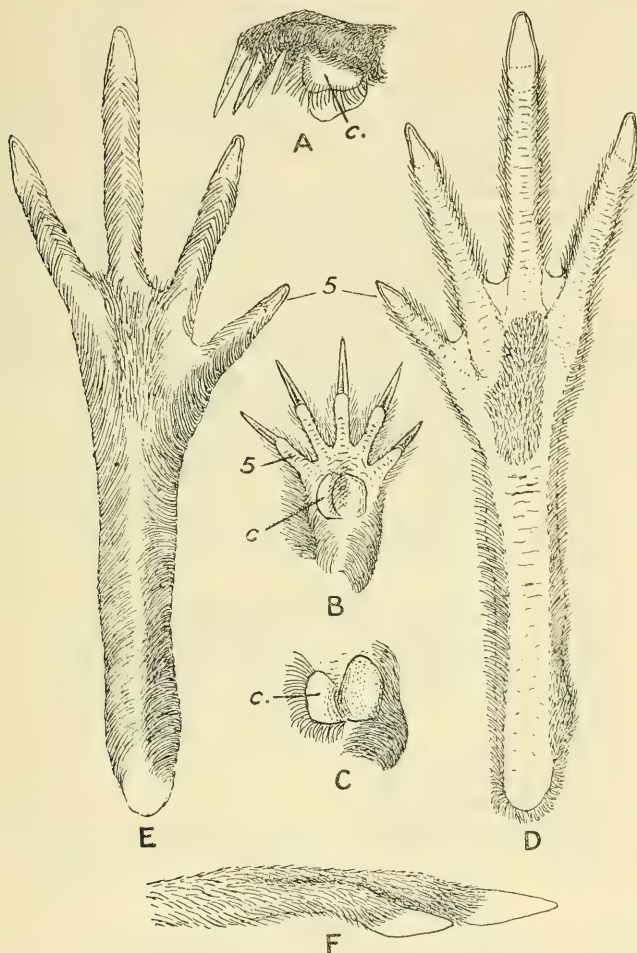
- A. Right hind foot of *Scarturus tetradactylus*, from outer side.
- B. Lower view of same, with digits closed together.
- C. Right hind foot of *Allactaga indica*, from outer side.
- D. The same of *Scirtopoda orientalis*.
- E. Lower view of the same, with digits closed.

The hind foot of *Pedetes*, although saltatorial, has the metatarsus much shorter in relation to the length of the digits than in the Jaculidæ; but it resembles the hind foot of the latter in having the third digit the longest, set in the middle line, and flanked on each side by the second and fourth; and, as in the Jaculidæ, the under side of the digits and mostly of the metatarsus is naked, but covered with the hairs which overlap them from the sides. As in *Scarturus*, there are four digits, the first having entirely disappeared, while the fifth is retained. But, apart from

\* The only specimen examined had been for many years in alcohol, and possibly the pads were shrunken in size.

these features, the foot is very different from that of all the genera of Jaculidæ. For instance, the fifth digit forms a uniform series

Text-figure 35.



- A. Left fore foot of *Pedetes caffer*, from outer side.  
 B. Right fore foot of the same, from below.  
 C. Two carpal pads of the same, spread (on rather larger scale).  
 D. Right hind foot of the same, with hairs cut short.  
 E. Left " " " with hairs entire.  
 F. The same from outer side, showing fourth and fifth digits.

c., outer movable carpal lobe with fringe of hair; 5, fifth digit.

with the next, the space between it and the fourth being equal to that between the fourth and third or third and second,

Again, the claws are broad and strong like pointed hoofs, and beneath are completely fused with the digital pads, which are represented merely by an ill-defined area constituting the heel of the hoof. I can find no trace of plantar pads, although Tullberg describes one at the base of each digit. All that I can find is an elevation at the base of each digit formed by the underlying bone. That, however, does not constitute a pad. The middle area of the foot behind the base of the digits is provided with a mat of long hairs which functionally takes the place of the plantar pad. Behind this the sole is naked up to and including the heel. (Text-fig. 35, D-F.)

Good characters for distinguishing the families, subfamilies, and the principal genera are supplied by the hind feet:—

- |                                                                                                                                                                                                                                                                                                                                                                                                                           |                             |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------|
| a. Claws broad and hoof-like; digital pads scarcely developed, merely forming an ill-defined heel to the hoofs; plantar pads suppressed, their place taken by a mat of hairs above the base of the digits ...                                                                                                                                                                                                             | <i>Pedetes.</i>             |
| a'. Claws sharp and curved, not hoof-like; digital pads normally or exceptionally developed; plantar pad present, the middle of the foot above the base of the digits naked.                                                                                                                                                                                                                                              |                             |
| b. Foot with separated metatarsals, "murine," artiodactyle or nearly so; plantar pad represented by four interdigital papillæ; hallux much smaller than fifth digit and higher up the foot, the fifth at least reaching the base of the fourth; digital pads normal.                                                                                                                                                      |                             |
| c. Foot short with digits 2 to 5 subequal, subequally spaced, and terminally almost in a line; plantar and metatarsal papillæ comparatively large .....                                                                                                                                                                                                                                                                   | <i>Sicista.</i>             |
| c'. Foot long, with third and fourth digits terminal and close together, the second farther from the third, and the fifth still farther from the fourth; plantar and metatarsal papillæ minute.....                                                                                                                                                                                                                       | <i>Zapus.</i>               |
| b'. Foot with three median metatarsals fused, very long, not "murine," markedly perissodactyle; plantar pad represented by a single median conical papilla; hallux, when present, as large as the fifth digit and set on the same level, so high up the foot that their tips fall far short of the bases of the adjoining digits; digital pads of second to fourth large, deep, compressed, and deeply grooved laterally. |                             |
| d. Fifth digit retained; short fringes of hair on digits 2 to 3; plantar papilla very large and exposed*.                                                                                                                                                                                                                                                                                                                 |                             |
| e. First digit (hallux) retained .....                                                                                                                                                                                                                                                                                                                                                                                    | <i>Allactaga.</i>           |
| e'. First digit (hallux) absent.....                                                                                                                                                                                                                                                                                                                                                                                      | <i>Scarturus.</i>           |
| d'. Fifth digit absent; long fringes of hairs on digits 2 to 3; plantar papilla very small, normally concealed by overfolded fringes of hair .....                                                                                                                                                                                                                                                                        | <i>Jaculus, Scirtopoda.</i> |

### Tails.

In *Sicista* and *Zapus* the tail is long, subcylindrical, tapering, and covered with scales and short hairs as in typical murine Rodents, the hairs at most forming a slight terminal pencil. In the majority of the *Jaculidæ* it is more definitely quadrate, covered with short hairs, not distinctly scaly, and is provided with a distinct terminal tuft, which, however, varies considerably in size. In *Jaculus jaculus*, *Scirtopoda orientalis*, and *Scarturus*,

\* The hairiness of the feet in *Allactaga* may vary specifically according to habitat.



for instance, the hairs of the tuft are long and show a marked tendency to a bilateral, distichous, or feather-like arrangement, apparently to give support and prevent the end sinking into soft sand when used as a prop; and probably for use as a guide-mark in the dark, the tuft is usually conspicuously black or brown and white, the distal half being white and the proximal black or deep brown, and frequently additional white hairs precede the dark-coloured portion. The size of the tuft, however, varies even within specific limits. It is, for example, very large in *Allactaga saliens* Gm. (= *jaculus* Pall.) and quite small in *Allactagulus acontion* Pall. and *Allactaga elater* Pall., judging from Lichtenstein's figures. In the two first-mentioned, moreover, it is conspicuously coloured, whereas in the last it appears to be uniformly or nearly uniformly brown. In *Euchoreutes*, according to Selater, it is moderately developed and bicoloured, but "the hairs do not seem to be arranged in so distichous a manner as in *Allactaga*."

Two genera, however, of this family—namely, *Pygeretmus* and *Cardiocranius*—have the tail of a very different shape. It is narrow and cylindrical at the base, then broadened, depressed, and lanceolate, with the apex attenuate, but not tufted at the end as in typical Jerboas. Thus two distinct types of tail are found in the Jaculidæ.

In *Pedetes* the tail is long and bushy throughout, being uniformly and thickly covered with long hairs from base to apex.

#### Summary of the Characters of the Tails.

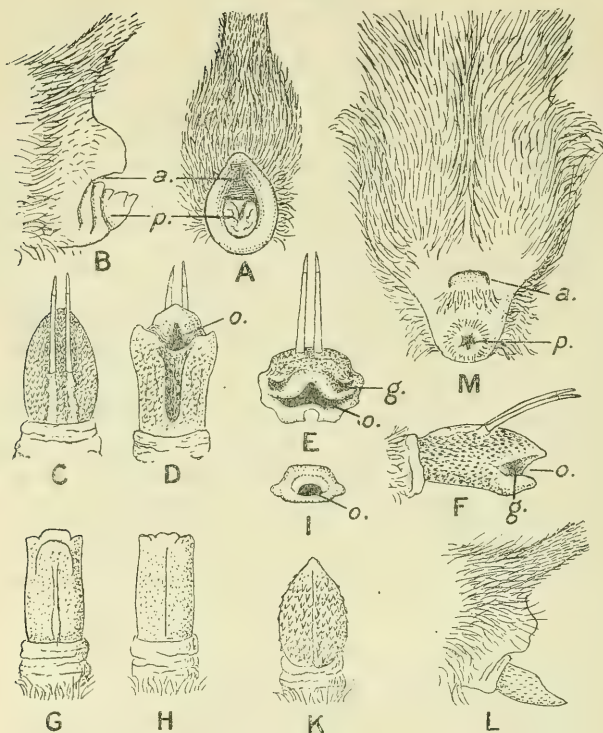
- a. Tail subcylindrical or subquadrate.
- b. Tail uniformly and thickly covered throughout with long hairs... *Pedetes*.
- b'. Tail covered for the most part with short hairs, often tufted at the end.
- c. Tail covered with short hairs and rows of scales, at most pencilled at the end ..... *Sicista*, *Zapus*.
- c'. Tail covered with hairs, but not visibly scaly, with larger or smaller terminal tuft ..... *Jaculus*, *Scirtopoda*, *Scarturus*, *Allactaga*, *Euchoreutes*.
- a'. Tail broad, flattened, and lanceolate, covered with short hairs, apically pencilled, not visibly scaly ..... *Pygeretmus*, *Cardiocranius*.

#### *Anus and External Genitalia.*

In *Zapus* the anus, as in most Rodents, opens in the centre of an area of naked skin above the genital orifice, the two orifices being separately visible on superficial inspection. In the female the vulva is, however, just below the anus and the naked skin surrounding it is continuous above with that surrounding the anus. There is no elongated, conical, preputial excrescence and no visible external clitoris. In the male the penis, normally retrospective, is separated by a fringe of hair from the anus



## Text-figure 36.



- A. Rear end of *Scirtopoda orientalis*, from behind, with the anal lobe raised to show the anal orifice (a.) above the penis (p.).
- B. The same from the side, with the anal lobe in natural position and the penis (p.) partially protruded.
- C. Upper side of glans penis of *Scirtopoda orientalis*, with spikes lying forwards.
- D. Lower view of glans penis of the same, with apex dilated.
- E. Dilated tip of glans penis of the same from the front, with spikes raised.
- F. Side-view of glans penis of the same, with spikes partially raised.
- G. Upper view of glans penis of *Jaculus jaculus*.
- H. Lower view of the same.
- I. Tip of glans penis of the same, from the front.
- K. Upper side of glans penis of *Scarturus tetradactylus*.
- L. Rear end of *S. tetradactylus*, with glans partially protruded.
- M. Rear end of *Pedetes caffer*, from behind, with crescentic anus above penis.

a., anus; g., glandular pit in penis of *Scirtopoda orientalis*; o., genito-urinary orifice; p., penis.

above, and its glans is slender and subcylindrical, according to Tullberg\*.

In all the specimens of *Jaculidæ* examined the anal and generative orifices are so closely applied that on superficial inspection there appears to be a single orifice only, situated upon a thick naked excrescence a little distance below the root of the tail. In the females, indeed, the vulva and anus are slightly insunk, and are closed by a common sphincter. In the males the tip of the penis in its natural position is pressed up against the lower side of the anal prominence which carries the anal orifice, concealed from view, on its underside. This prominence is exceedingly large in *Scirtopoda orientalis* (text-fig. 36, A, B).

The penis of *Scirtopoda orientalis* was first described by Sonnini† and Olivier‡. The glans is large and oval in shape, and is thickly covered with many backwardly directed short spines; but, in addition, it is armed with a pair of long slender stiliform spikes, like those in the pouch of the glans of *Cœlogenys*, *Cavia*, and some other Hystricomorphs. These spikes are rigid, except at the tips, which are soft. According to Sonnini, these tips form a small yellow button like the anthers of certain flowers; but in the specimens examined by me they were pointed and only distinguishable by their softness from the rest of the spike. Normally these spikes lie forwards upon what is the upper side of the penis when this organ is extended from the prepuce and directed forwards, and their tips overlap the apex of the glans; but they are capable of being elevated or even directed backwards. Beneath the narrowed apex of the glans the large orifice, which has an upper and a lower lip, opens, and on each side of it there is a shallow, probably glandular, pouch. The lower side of the glans is provided with a median, probably glandular, gutter, the edges of which, when brought together, form a narrow lineal crease (text-fig. 36, C-F). In *Jaculus jaculus* the glans penis is very different, as Anderson and de Winton pointed out. It has no spikes; and the small spines seen in *Scirtopoda orientalis* are represented by minute pits, in each of which there is sunk a scale with serrulate free edge. There is a median thickening on what is the upper side of the penis when this organ is turned forwards, and there is a narrow median groove below. There is a curved groove above the upper lip of the orifice and a small prominence on each side of it, but no glandular depression. (Text-fig. 36, G-I.)

In *Scarturus* the glans is oval or cordate from above or below, pointed from the side-view, and the terminal orifice is simple. It is armed with sharp recurved spines, which are fewer in number and relatively larger than in *Scirtopoda orientalis*, but there is

\* In the specimen I examined the tip of the glans was covered with an extraneous thickening of hard material closely adherent to it.

† Voy. en Egypte, i. pp. 173-174 (1800).

‡ Bull. Soc. Phil. Paris, ii. no. 40, p. 121 (1801).

no trace of the pair of long spikes seen in the latter species. According to the descriptions of Olivier and Tullberg the glans penis of *Allactaga sahensis* closely resembles that of *Scarturus*. (Text-fig. 36, K, L.)

The anus and genitalia of the male of *Pedetes caffer* were described and figured by Calori\*. To his account Tullberg had nothing to add. The anus is situated a long way below the root of the tail, much farther than in the *Jaculidæ*, and the prepuce of the retroverted penis forms a conical prominence beneath it. Superficially the anus appears as a crescentic slit, with the concavity downwards; and this appearance results from the downward growth of the skin of its upper border forming a flap over the anus itself. Calori described a gland-opening in the middle line of the perineum between the anus and the penis. This does not appear to me a very appropriate description, because no orifice is visible on the area named. There is, however, the orifice of a gland-opening within the prepuce just above the urino-genital orifice when the penis is retroverted and at rest. The penis itself is elongated, compressed, and covered with minute spicules; but there is no trace in it of the glandular pouch which is so characteristic of the *Hystricomorphs*. (Text-fig. 36, M.)

- |                                                                                                                                                                                   |                              |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------|
| a. A large gland-opening within the prepuce of the male on the anal side of the genito-urinary orifice; anus in the form of a crescentic slit some distance above the penis ..... | <i>Pedetes.</i>              |
| a'. No preputial gland on the anal side of the genito-urinary orifice of the penis; anus not crescentic in shape.                                                                 |                              |
| b. Anus exposed above the tip of the penis, which is not tucked up against it.....                                                                                                | <i>Zapus.</i>                |
| b'. Anus concealed beneath an excrescence, to the under side of which the tip of the penis is applied.                                                                            |                              |
| c. Glans penis spiny with two immense erectile spikes .....                                                                                                                       | <i>Scirtopoda.</i>           |
| c'. Glans penis without spikes.                                                                                                                                                   |                              |
| d. Glans penis elongated, parallel-sided, covered with minute pits, each provided with a serrate scale .....                                                                      | <i>Jaculus.</i>              |
| d'. Glans penis ovate, armed with spines .....                                                                                                                                    | <i>Scarturus, Allactaga.</i> |

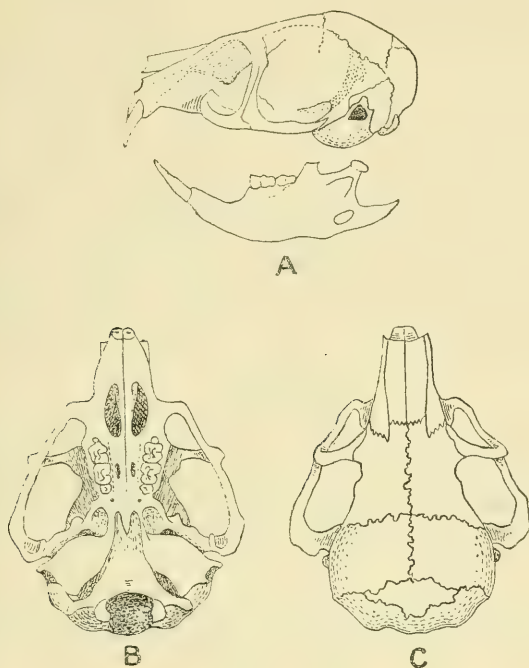
### *The Skull of Scarturus.*

The skull and dentition of *Scarturus* agree in essentials with those of *Allactaga*, and differ in many points from those of *Jaculus*—that is to say, the incisors are ungrooved and slightly projecting, though not nearly so strongly as in *A. indica*, for example; the minute upper premolar is retained; the zygomatic arch is comparatively slender where it forms the anterior wall of the orbit; the channel for the nerve is formed by a deep notch in the floor of the antorbital foramen and not a closed tube as in *Jaculus*; the auditory bullæ are much less inflated than in *Jaculus*, despite the large size of the ears, and the mastoid is not visibly inflated. I cannot, indeed, find any generic characters to

\* Mem. Accad. Sci. Bologna, v. pp. 297-298 (1854).

distinguish the skull of *Scarturus* from that of *Allactaga*, unless it be the lesser prominence of the incisor teeth and the presence of

Text-figure 37.



- A. Skull of *Scarturus tetradactylus*, from the side.  
 B. The same, from below. The molar teeth which were out of the skull are diagrammatically represented.  
 C. The same, from above.

a longish median process projecting backwards from the palate over the mesopterygoid fossa, a character observed in the one skull of *Scarturus* examined.

#### *The Genus Scirtopoda Brandt.*

In his selections of the type-species for some of the genera and subgenera introduced into the family Jaculidæ by the older authors, Thomas cited *Dipus mauritanicus* Duv. as the typical representative of Brandt's genus *Scirtopoda* and also of its subgenus *Haltomys* (Ann. Mag. Nat. Hist. (8) ii. p. 308, 1908). He also stated that *mauritanicus* is identical with or closely allied to the large Egyptian Jerboa described by Olivier as *Jaculus gerboa*, the species quoted as *Jaculus orientalis* in the preceding pages of this paper. Except that the ears are relatively and the bodily size actually larger in this species than in *Jaculus jaculus* and the

colour slightly different, I can find no difference between the two in external characters to which I should attach generic value. In dentition and cranial characters they are also much alike. But the external genitalia of the male are profoundly different. In my opinion these differences are of greater systematic importance than the cranial and dental characters employed for separating generically such forms as *Jaculus jaculus* and *Dipus sagitta*\*. I propose, therefore, to resuscitate the genus *Scirtopoda* Brandt, separating it from *Jaculus* by the peculiar armature of the glans penis.

I am not in a position to give an opinion as to the suggested identity between *S. mauritanicus* and *S. orientalis*; but Duvernoy's and Lereboullet's figures and description of the penis of *mauritanicus* (Mém. Soc. Mus. Strasbourg, iii. no. 2, p. 48, pl. iv. fig. 12, 1842) show that that organ is of precisely the same nature as in *orientalis*. The spikes on the penis appear, indeed, to be shorter in *mauritanicus* than in *orientalis*, but that may be merely an individual difference.

### Conclusions.

The analytical keys published in the foregoing pages to show the incidence of the genera according to the characters described attest the isolation of *Pedetes* from the rest of the genera, and thus bear out the prevalent opinion of the present day that that genus is in no way related to the Jerboas and Jumping Mice. *Pedetes*, therefore, need not be considered further in the present connection.

The keys also bear witness to the affinity nowadays admitted to exist between the Jerboas and the Jumping Mice, but show that the two may be sharply distinguished by the structure of the hind feet.

In 1901 Lyon (Proc. U.S. Nat. Mus. xxiii. p. 666), using skeletal (mainly cranial and dental) characters, classified the Jerboas and Jumping Mice as follows:—

#### Family ZAPODIDÆ.

Subfamily SMINTHINÆ (*Sminthus*, ? *Eomys*).

„ ZAPODINÆ (*Zapus*, *Napæozapus*, *Eozapus*).

#### Family DIPODIDÆ.

Subfamily DIPODINÆ (*Dipus*, *Allactaga*, and probably *Platycomys*).

„ EUCHOREUTINÆ (*Euchoreutes*).

\* I am aware that the use of soft parts for differentiating genera of Mammals may be an annoyance to modern systematic mammalogists, who, following the fashion set in the United States, like to work from dried skins and skulls. But, although the zoo-geographical and other results obtained from that method are of great value and interest, I am sure that the sooner the swing of the pendulum carries us back to the method in vogue thirty years ago of working from fresh or spirit-preserved material, combined with skins, the better it will be for the science of mammalogy.



Apart from the alterations necessitated by the nomenclature now in vogue and the addition of several recently proposed or recently restored generic names to the Jerboa family, I have no modifications of this classification to suggest, except the severance from the rest of the Jerboas of the two genera *Pygeretmus* (*Platycomys*) and *Cardiocranius*\*, which agree in having broad, flattened, lanceolate tails, distinguishing them at once from the rest of the family. They may constitute the subfamily Pygeretminæ, which appears to be a specialised offshoot of the five-toed *Allactaga*-group. The two genera differ at least in the following characters:—*Pygeretmus* has lost the anterior upper premolar, which *Cardiocranius* retains; the latter has grooved, the former ungrooved upper incisors.

Lyon divided his Dipodinæ into two groups: (1) *Dipus*, with its subgenera, possessing three toes, a considerably inflated mastoid, the upper incisor grooved, the anterior upper premolar absent, and the antorbital canal for the nerve complete. (2) *Allactaga*, with its subgenera, has more than three digits, the mastoids not much inflated, the upper incisors without grooves, the small anterior upper premolar present, and the antorbital canal for the nerve incomplete.

If the above-mentioned characters held good there would be strong reasons for separating *Allactaga* and its kindred from *Dipus* and its allies as a special subfamily Allactaginæ. But there seem to be too many intermediate forms to make such a course advisable. In the number of the toes, for instance, *Scarturus* is precisely midway between *Dipus* or *Jaculus* and *Allactaga*. In the Asiatic three-toed Jerboa, *Dipus* †, the mastoids are much less inflated than in the African forms, *Jaculus* and *Scirtopoda*; *Dipus* thus connects those genera with *Allactaga* in that particular. In *Dipus*, too, the anterior small premolar is retained as in *Allactaga*, whereas it is lost in *Jaculus* and *Scirtopoda*. On the other hand, the small five-toed Asiatic Jerboa, *Allactagulus acontion*, resembles the three-toed African genera, *Jaculus* and *Scirtopoda*, in the loss of this molar.

Of the characters mentioned by Lyon, therefore, there remain as distinctive only the presence or absence of the grooves in the

\* Satunin, Ann. Mus. Zool. St. Petersb. 1902, p. 582. The genus *Cardiocranius* has an extraordinarily wide and inflated cranial portion of the skull, which, as compared with the facial portion, is much larger even than in *Euchoreutes*. I associate this genus with *Pygeretmus* on the assumption that the peculiarly modified tail has not been developed twice independently within the group.

† For the sense in which this genus is here used, *sagitta* being its type-species, see Thomas, Ann. Mag. Nat. Hist. (8) ii. p. 308 (1908). Trouessart seems to have been unaware of this paper by Thomas when he published his 'Faune des Mamm. d'Europe' in 1910. At all events, he proposes the new name *Dipodipus* for the group of Asiatic three-toed species, with *sagitta* as the type, for which Thomas showed the old name *Dipus* to be available. Satunin seems to have come independently to the same opinion on this point as Thomas (Mitth. Kankas. Mus. 1907, p. 72). Trouessart also resuscitated *Scirtopoda* in quite a different sense from that in which Thomas employed it (cf. *supra*, p. 679). But, since Thomas was the first reviser of the nomenclature of these Jerboas, I follow his decisions.

upper incisor teeth and the closed or open canal for the antorbital nerve. I am not aware whether these are constant differences.

Adopting Lyon's classification with the modifications above mentioned, the families and subfamilies of Jumping Mice and Jerboas will be as follows:—

I. Family ZAPODIDÆ.

1. Subfamily SICISTINÆ \* = SMINTHINÆ (*Sicista*).
2. „ ZAPODINÆ (*Zapus*, *Napæozapus*, *Eozapus*).

II. Family JACULIDÆ OR DIPODIDÆ.

1. Subfamily JACULINÆ OR DIPODINÆ (*Jaculus*, *Scirtopoda*, *Dipus*, *Scarturus*, *Allactaga*, *Alactagulus*).
2. „ PYGERETMINÆ (*Pygeretmus*, *Cardiocranius*).
3. „ EUCHOREUTINÆ (*Euchoreutes*).

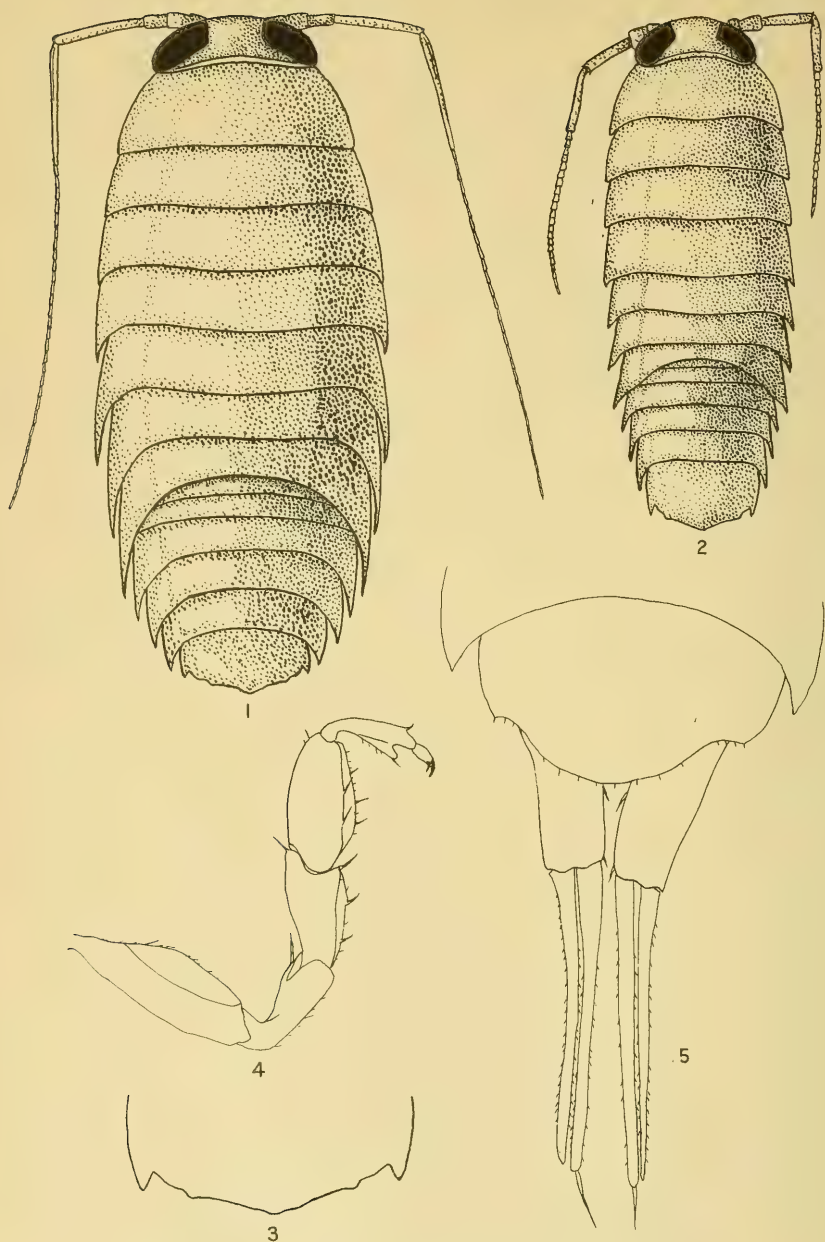
The chief distinguishing characters of the Zapodidæ and Jaculidæ and of the Sicistinæ, Zapodinæ, and Euchoreutinæ may be found in Lyon's paper. Those of the Pygeretminæ are stated above. With regard to the Jaculinæ, the genera which appear to me to be admissible, though there may be others, may be distinguished as follows:—

- |                                                                                               |                      |
|-----------------------------------------------------------------------------------------------|----------------------|
| a. Five or four toes on the hind foot; incisors ungrooved; antorbital nerve-canal open above. |                      |
| b. Five toes on foot, hallux present.                                                         |                      |
| c. Small upper premolar retained .....                                                        | <i>Allactaga</i> .   |
| c'. Small upper premolar lost .....                                                           | <i>Alactagulus</i> . |
| b'. Four toes on foot, hallux lost (skull and dentition as in <i>Allactaga</i> ) .....        | <i>Scarturus</i> .   |
| a'. Three toes only on hind foot; incisors grooved; antorbital canal closed above (? always). |                      |
| d. Small upper premolar retained; mastoids less inflated .....                                | <i>Dipus</i> .       |
| d'. Small upper premolar lost; mastoids much inflated.                                        |                      |
| e. Glans penis without spikes, with insunk scaly armature .....                               | <i>Jaculus</i> .     |
| e'. Glans penis with a pair of large erectile spikes and spinous armature .....               | <i>Scirtopoda</i> .  |

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\* See Miller, Cat. Mamm. Western Europe, p. 536 (1912).

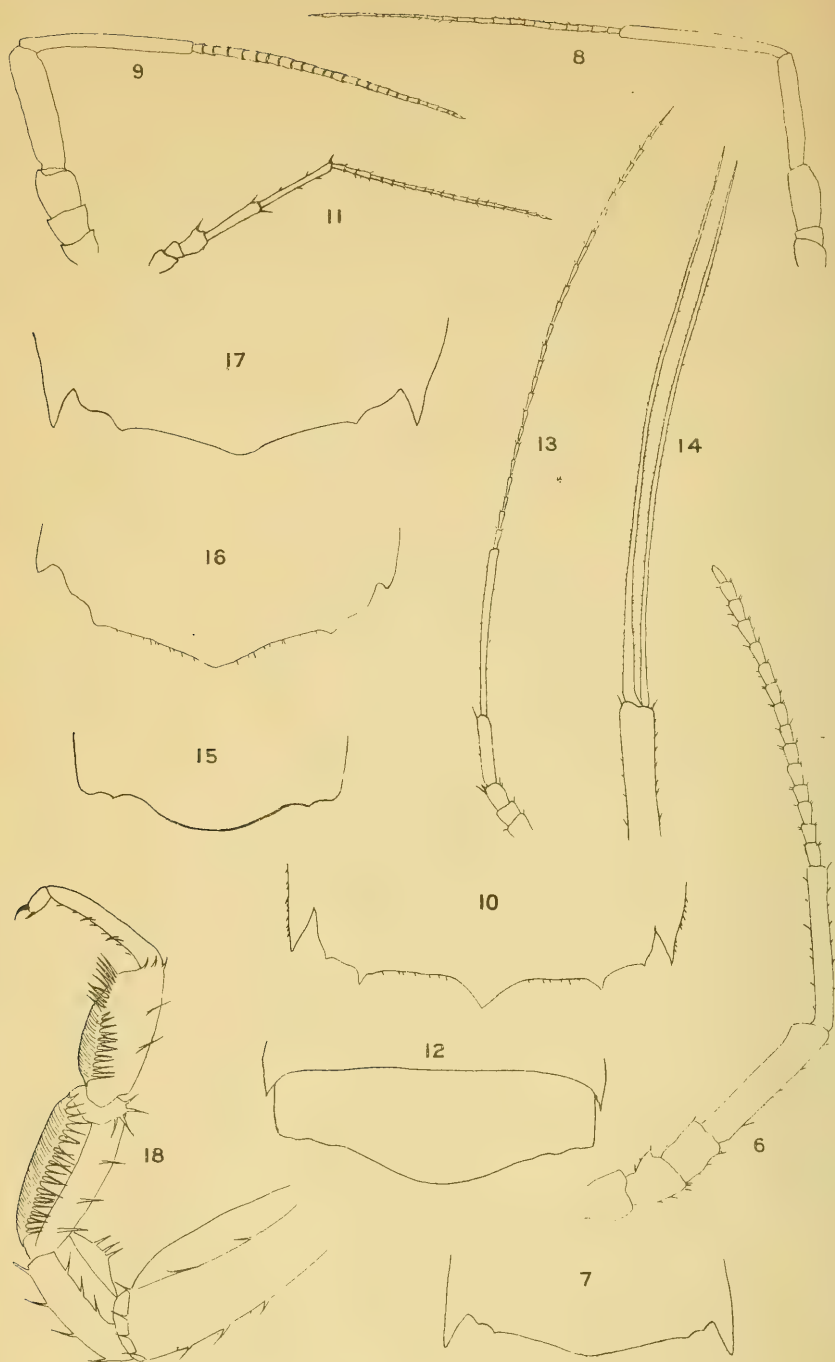




REVISION OF THE GENUS *LIGIA* (FABRICIUS).







REVISION OF THE GENUS *LIGIA* (FABRICIUS).

35. A Revision of the Isopod Genus *Ligia* (Fabricius). By  
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(Plates I. & II.\*)

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(1) *Preface.*

This paper on the genus *Ligia* is intended to be the first of a series dealing with the Terrestrial Isopods. The opportunity of undertaking the work was given to me by Dr. W. T. Calman, F.R.S., who placed at my disposal the material, now in the possession of the British Museum, which belonged to the late G. Budde-Lund. The author of 'Isopoda Terrestria' evidently intended to use this material, which comprises specimens of most known species of terrestrial Isopods, for the revision of his great work on which he was engaged at the time of his death. He was only able to complete the genera *Eubelum*, *Armadillo*, and the subfamily Spherilloninae, but he left notes of observations on other genera which will be referred to in their proper place. I propose

\* For explanation of the Plates see p. 703.

to endeavour to carry on, from the place at which it was left by Budde-Lund, the task of making a critical revision of the 'Isopoda Terrestria,' with the aid of his collection and other material in the Museum.

I should like here to pay tribute to the generosity with which Dr. Calman has always put his unrivalled knowledge of the Crustacea at my disposal during this investigation; my grateful thanks are also due to my wife for many of the figures illustrating this paper and a great deal of other tedious work, and to Mr. Frank Forty for his excellent figures of *L. pigmentata* and *L. perkinsi*.

## (2) Introduction.

Budde-Lund recognised seventeen species in the genus *Ligia*, five of which he had not seen and therefore did not describe. Since the publication of 'Isopoda Terrestria' several new species have been created, three of which still stand, some of the doubtful species have been set on their feet, and the genus *Geoligia* has been created to contain two purely terrestrial Ligiidæ. Budde-Lund's descriptions were always in Latin and, valuable as they are, were often extremely sketchy; and no serious attempt was made to describe thoroughly any species of *Ligia* until Sars in 1899 gave his classic diagnosis and figures of *Ligia oceanica*. Later, in 1901 and 1916, Chilton did an equally admirable service for *Ligia novæ-zealandiæ* and *exotica*. Not all modern descriptions have improved greatly on their predecessors, although Miss Richardson has given careful accounts of the American species of *Ligia*.

Having had the privilege of examining an extended series of forms, I have been in a very favourable position for weighing the relative importance of various characters in discriminating between species. In descriptions of new species, characters are again and again cited as specific which are found on examination to be generic, but not referred to—either being considered as unimportant or not having been noticed—by previous authors. For example, such a careful and reliable writer as Chilton gives "transverse depression just posterior to the angle of the eye, interrupted in the middle" as a specific character of *Ligia novæ-zealandiæ*, when, in fact, there is no *Ligia* of any species I have seen in which this "depression" is absent.

## (3) Sexual Characters.

The very marked sexual differences have been a stumbling-block in the recognition of genuine species.

The secondary sexual characters in which the sexes differ are as follows:—

1. The antennæ of the male are usually relatively longer than those of the female and are frequently stouter, though not in all species.

2. The pereopods often possess well-marked processes or spines in the male only, and also frequently bear a plate-like expansion covered with file-like serrations on two or more segments of the first two or three legs, as has already been remarked by Chilton in *Ligia oceanica* (1899). The feature is constant enough to justify the conjecture that it is of value in holding the female in pairing.

3. The sutures between coxal plates and terga are frequently well marked on the dorsal surface of three or more segments of the thorax of the female, but in the male there is rarely more than the faintest indication of the suture. This character will be referred to in detail in the description of each species and in the discussion on *Geoligia*.

4. The male is usually larger than the female, but frequently relatively narrower; doubtless this difference is associated with the brood-pouch of the latter.

It follows from this that descriptions of species founded on any of the above characters, in which the sex is not named, must be looked upon with suspicion. As far as possible I have always noted in the following pages characters in which the sexes differ, or have stated on which sex the description has been based.

#### (4) *Generic and Specific Characters.*

Nearly every external character possessed by *Ligia* has been used from time to time for systematic work. As these characters are of very unequal value, I will pass them in review and endeavour to justify the characters on which I have based my descriptions.

The *proportions* of the body and the *size* vary with age and sex, but bearing that in mind, they may be a valuable guide.

The shape of the *somites* of the body differs very little in the different species. As a rule the hinder margins of the first three thoracic somites are transverse and the remainder progressively more and more curved, and the coxal plates are drawn out into progressively longer backwardly-directed spines. The first three or four somites of the thorax are about equal in length and the others successively shorter. Unless there is any strongly marked difference, I have therefore omitted these points in my descriptions.

The *general shape* of the body cannot be described in other terms than "elongate-oval" or the like, so it is unnecessary to repeat it for each species.

The *colour* in the case of preserved specimens, especially if they have been kept in spirit a long time, is almost valueless.

The *surface* of the body is always covered with minute granulations, and the free margins of the somites are beset with minute setæ, but in some species the surface is notably smoother than in others.

The *cephalon* has a transverse groove on its hind border and two somewhat pear-shaped post-orbital pits ("interrupted depression" of Chilton). There are three transverse grooves on the epistome in all species.

The eyes of the same species have been described by different authors as "moderate," "large" or "small." Compared with some nearly related genera, the eyes of any *Ligia* would be large: it is therefore unnecessary to do more in a specific description than compare one species with another.

The *abdomen* (metasome) has the first two somites covered by the last thoracic and without the drawn-out pleural plates possessed by the remaining somites. The difference in width between abdomen and thorax is more marked in some species than in others, but I cannot consider it a good character, as it is distinctly affected by the preservation of the specimen; when the body is flaccid and the anterior abdominal somites are more exposed, the difference is exaggerated. In many species there are indications of lateral oblique carinæ on the third, fourth, and fifth abdominal somites. I have noted the character when it is conspicuous.

The *terminal segment* (telson + 6th abdominal somite) varies slightly with every species and is, therefore, a valuable character. The posterior margin may be produced into spines or blunt processes. It may bear a *median process* which may be acute or almost obsolete; the corners may be drawn out into *postero-lateral processes*. On each side above the point of insertion of the uropod the margin may bear two processes (sometimes little more than undulations), the *inner* and *outer accessory processes* (Pl. II. fig. 10).

The key given on p. 689 is based in the first place on the shape of the posterior margin between the two inner accessory processes. If a median process is present, the margins on either side of it, between it and the inner accessory processes of each side, are always, however slightly, concave. Long usage has sanctioned for this type of telson the inaccurate term "triangulate."

On the other hand, an "arcuate" margin is smoothly convex between the inner accessory processes.

It is conceivable that cases may arise which are intermediate between the two types, but the material described below presents no difficulties.

The appendages are of great systematic value.

The *first antennæ* are vestigial throughout the genus.

The *second antennæ* differ greatly in length, in the character of the segments of the flagellum and in the relative length of the peduncle and flagellum. I have followed Miss Richardson in describing the length of the appendage in relation to the somites of the body, but I cannot follow her in attaching importance to the relative length of the segments of the peduncle. The number of segments of the flagellum is useful as a general indication, but as it sometimes differs on the two sides of the same animal, it must not be taken too seriously.



The *mouth-parts* differ slightly throughout the genus. It is interesting to note that in the majority of species the maxillipede (whose palp has always five separate or indicated joints) and second maxilla differ from those of *Ligia oceanica*, the type of the genus. The first maxilla and the mandible are, however, very constant in structure, on which account I have considered it unnecessary to deal with them under each species.

The *peraeopods* are always biunguiculate. In the males of certain species the inner edges of the first and sometimes second and third leg are deeply sulcate. I have not enough material to pronounce on the value of this character, but as I have found it present in some and absent in other specimens collected at the same spot and obviously identical in all other particulars, I feel it necessary to regard it with caution until its significance is known. The sexual differences have been alluded to above.

I have not found the *pleopods* to be of any systematic value.

The *uropods* are frequently distinctive both in shape and size.

### (5) *The genus Geoligia.*

This genus was founded by Dollfus in 1893 on a single damaged male specimen obtained from Valencia (Venezuela) at a height of 1200 metres above sea-level. The character on which the genus was separated from *Ligia* was the absence of indication of separation of coxal plates from terga on the thorax, added to the unusual habitat of the specimen.

In 1900 the same author described specimens from the Hawaiian Islands, obtained at heights varying from 2000 feet to 4000 feet, as a new species of the same genus. These differed from the holotype in many particulars, and one male specimen was in possession of a complete uropod of extraordinary form, the rami being composed of several segments. Dollfus accordingly added to the characters of the genus the possession of jointed uropods, and his diagnosis is as follows:—

“Coxopodites (épimères) non ou très peu distincts.  
Appendices des uropods articulés. Le reste, et notamment les parties buccales, comme dans le genre *Ligia*—espèces terrestres.”

An examination of the degree of separation of the coxal plates from the terga throughout the genus *Ligia* reveals that it would be a most treacherous character on which to found a species, let alone a genus. It is variable, even within a species, but a generalisation that would be true for the majority of cases might be stated thus:—The sutures between the coxal plates and terga are always visible to a greater or lesser extent in the female on the second, third, and fourth thoracic somites; they may be present or absent on the other somites. In the male the sutures may be altogether obliterated (e.g. *L. olfersii*) or well marked on each thoracic somite (e.g. *L. oceanica*).

The original specimens of the Hawaiian *Geoligia perkinsi* are preserved in the British Museum. An examination of the material shows that any generic distinction based on this character must be abandoned, as the females all have this suture well marked on the second, third, and fourth somites.

An examination of the single uropod cannot but raise doubts as to the genuine nature of the "joints." These are at most irregular intervals, and show under a high magnification no arthrodial modification of tissue such as would be found in a natural structure.

It is therefore suggested that the segments of the rami were produced accidentally. Among two dozen specimens of *Ligia exotica*—a species distinguished by the length and slenderness of the uropods—I found two specimens which showed "joints" in the rami, identical in every respect with those of *Geoligia perkinsi*. Further, when placed side by side with a uropod which had been purposely bent, no difference could be detected. The probability that the jointed uropod of *Geoligia* is of accidental origin is therefore exceedingly strong, and the last anatomical difference between *Geoligia* and *Ligia* is thereby removed.

If *G. simoni* and *G. perkinsi* are compared, it will be found that they differ widely from one another in relative size of eyes and head, length of antennæ, shape of telson, and other points. The artificial nature of the genus is shown by the fact that they differ more from each other than each differs from certain species of *Ligia*, and difficulty arises in finding not generic but specific differences between these species and various species of *Ligia*.

In 1915, Pearse (p. 549) described under the name of *Ligyda richardsonæ*, specimens he collected in Cincinnati, Colombia, at 3800 feet elevation. This species greatly resembles *Geoligia simoni*, and occurs at no great distance from it, and it is very probable that collection of more material from Venezuela and Colombia will show that both must be referred to the same species. If habitat is to count for everything in the delimitation of genera, then Pearse should have made a new genus for *L. richardsonæ* or have placed it in Dollfus's genus, of which he seemed unaware. His action in retaining the genus *Ligia* for his new species supports my contention that bionomical considerations should have no weight in the separation of this genus from *Ligia*.

It may be assumed that these three species have arisen from littoral species of *Ligia* which have migrated inland and become slightly modified in so doing. Thus *Geoligia perkinsi* is almost identical with the littoral *L. hawaiiensis*, but *G. simoni* and *L. richardsonæ* present a more difficult problem, as the adjacent littoral species that have been recorded (*L. baudiniana* and *L. olfersii*) do not bear any obvious relation to them. Either they are modified from the *baudiniana* or from an unrecorded New World species resembling *L. italica*, from which they can only with difficulty be distinguished.





1. *LIGIA OCEANICA* (Linnæus).

*Ligyda oceanica* Richardson (1905), p. 684 (*q. v.* for complete synonymy).

*Ligia oceanica* Dahl (1916), p. 32.

Male specimen described.

*Length* 25 mm. *Breadth* 12 mm.

*Surface* moderately coarsely granulated. *Eyes* of moderate size, rounded and separated by twice their horizontal length. *Antennæ* moderately long and stout; flagellum reaching as far as the hind border of the 4th thoracic somite, the peduncle half-way down the 2nd somite. Flagellum with 12 to 14 very short and stout segments. *Coxal plates* divided by very distinct grooves from terga of every thoracic somite in both sexes. *Abdomen* not abruptly contracted. *Telson* arcuate; the postero-lateral processes acute and nearly as long as the middle of the hind border; accessory processes not produced, but the inner forming a prominent undulation. *Mouth-parts*: 2nd maxilla bilobed, with two hairy bristles on inner side. Maxillipede palp clearly divided into five joints. 1st *peræopod* of the male only has merus, carpus, and propodus produced on inner side to a flat plate-like expansion, with free border fringed with short setæ. The surface of this expansion is covered by oblique serrations. *Uropods* 7 mm.

*Distribution.* Hammershus; Cuxhaven; Portsmouth; Northern Seas. (See Richardson (1905) for complete list.)

Figured in full by Sars (1899).

2. *LIGIA PALLASII* Brandt. (Pl. I, fig. 4.)

*Ligyda pallasii* Richardson (1905), p. 682 (*q. v.* for synonymy).

*Ligyda pallasii* Richardson (1909), p. 125.

Male specimen described.

*Length* 35 mm. *Breadth* 20 mm.

*Surface* coarsely granulated. *Eyes* of moderate size, rounded and separated by twice their horizontal length. *Antennæ* moderately long and stout; flagellum reaching as far back as hind border of 5th somite, peduncle to hind border of 2nd somite; flagellum with 15 short and stout segments, without large setæ but densely covered with exceedingly minute setæ. *Coxal plates* divided by deep and distinct grooves on every thoracic somite in both sexes. *Abdomen* not abruptly contracted, with prominent oblique carinæ on each side of 3rd, 4th, and 5th somites. *Telson* arcuate; postero-lateral processes acute, produced as far as or beyond middle of hind border; accessory processes not produced, but the inner forms a prominent undulation. *Telson* twice as broad as long. *Mouth-parts* as in *L. oceanica*. 1st, 2nd, and 3rd *peræopods* with carpus and merus expanded as in *oceanica*. 2nd and 3rd legs with small process on propodus not reaching beyond the dactyl in both sexes. *Uropods* 8 mm.

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*Distribution.* Litycha; Alaska; California; British Colombia. (See Richardson (1905) for complete list.)

Figures in Richardson (1905).

This species is nearly related to the foregoing.

3. *LIGIA GLABRATA* Brandt. (Pl. I. fig. 5; Pl. II. fig. 6.)

*Ligia glabrata* Budde-Lund (1885), p. 263.

?*Ligia dilatata* Collinge (1920), p. 475.

Female specimen described.

*Length* 13 mm. *Breadth* 6 mm. (Another imperfect specimen measured 19 mm. by 9 mm.)

*Surface* very slightly granulated or nearly smooth. *Eyes* of small size, separated by about one and one-half times their horizontal length. *Antennae* of moderate length; flagellum reaching as far back as hind border of 5th thoracic somite, peduncle to hind border of 2nd segment; flagellum with 15 to 17 slightly setose, short, and squat segments. The *coxal plates* are divided by deep grooves on the 2nd, 3rd, and 4th thoracic somites. *Abdomen* not abruptly contracted. *Telson* arcuate; postero-lateral processes blunt and little produced; accessory processes almost obsolete. *Mouth-parts*: 2nd maxilla not bilobed, though a crease indicates the usual division; without hairy bristles on inner side. Maxillipede with 1st and 5th joints of palp distinct; remainder only indicated by deep marginal indentations. *Perceopods* typical in form. *Uropods* 4.5 mm.

*Distribution.* Cape of Good Hope; Table Bay.

Collinge (1920) surmises that *L. glabrata* is possibly an immature form of *L. dilatata*. These specimens are, however, undoubtedly mature, and must be identified with the former of Brandt's species. I have seen no male of this species.

4. *LIGIA OCCIDENTALIS* Dana. (Pl. II. figs. 7 & 8.)

*Ligyda occidentalis* Richardson (1905), p. 681 (*q. v.* for synonymy).

Male specimen described.

*Length* 25 mm. *Breadth* 11 mm.

*Surface* minutely granulated. *Eyes* large and quadrangular, and separated by less than the horizontal length of one eye. *Antennae* moderately long and slender; flagellum reaching as far back as hind border of 6th thoracic somite, peduncle to hind border of 2nd. Flagellum with 22 long and slender segments. Division of *coxal plates* lightly marked on all thoracic somites. *Abdomen* not abruptly contracted. *Telson* very obtusely tri-angulate; postero-lateral processes are as long as or longer than median process; accessory processes very small. *Mouth-parts*: 2nd maxilla weakly bilobed, with no hairy bristles; maxillipede with five distinctly marked joints. Propodus of 1st *perceopod* with prominent process on inner side of distal end, which projects forwards by the side of the dactyl. Carpus and merus of 1st and

2nd legs and carpus of 3rd flattened and striated as in *oceanica*.  
*Uropods* 10 mm.

*Distribution.* California; San Francisco. (See Richardson(1905) for complete list.)

Figures in Richardson (1905).

5. *LIGIA CINERASCENS* Budde-Lund. (Pl. II. fig. 9.)

*Ligia cinerascens* Budde-Lund (1885), p. 265.

*Ligyda cinerascens* Richardson (1909), p. 126.

Male specimen described.

*Length* 27 mm. *Breadth* 12 mm.

*Surface* minutely granular, rather smooth. *Eyes* large and nearly round, separated by their horizontal length or a little less. *Antennæ* moderately long and stout; flagellum reaching as far back as half-way across the 6th somite; the peduncle half-way across the 2nd; flagellum with 25 short and stout segments. *Coaxal plates* faintly indicated on all the thoracic somites of the male and very distinctly in the female. *Abdomen* not abruptly contracted. *Telson* broadly triangulate, the median process obtuse; postero-lateral processes produced to acute points reaching no further backwards than inner accessory processes; accessory processes slight but sharp. *Mouth-parts*: 2nd maxilla strongly bilobed, with two small hairy bristles on inner side; maxillipede with the five joints entirely separate. First *peræopod* with prominent inner process on propodus in male. *Uropods* 10 mm. + (rami broken).

*Distribution.* Hakodate, Japan; Manila or Chile.

This species is nearly related to *L. occidentalis*, but differs from it in the telson and the character of the antennæ. The segments of these are more numerous in *L. cinerascens*, but short and squat so that the whole appendage is relatively shorter than in *L. occidentalis*.

6. *LIGIA EXOTICA* Roux. (Pl. II. fig. 10.)

*Ligia dentipes* Budde-Lund (1885), p. 268.

?*Ligia malleata* Pfeffer (1889), p. 36.

*Ligia exotica* Budde-Lund (1908b), p. 303.

*Ligyda exotica* Richardson (1905), p. 676 (*q. v.* for complete synonymy).

*Ligyda exotica* Richardson (1909), p. 125.

*Ligia exotica* Budde-Lund (1912), p. 391.

*Ligia exotica* Chilton (1916), p. 462.

Male specimen described.

*Length* 27 mm. *Breadth* 17 mm.

*Surface* moderately roughly granulate. *Eyes* large and separated by less than their horizontal length. *Antennæ* very long and slender; flagellum reaching as far back as hind border of 5th abdominal somite, peduncle to hind border of 3rd thoracic somite. Flagellum with 28 or more very long and slender segments. The

antennais shorter in the female. The whole is as long as the thorax, and the peduncle reaches half-way across the 3rd somite. *Coxal plates* distinctly marked on all segments in both sexes. *Abdomen* not abruptly contracted. *Telson* with acute median process; postero-lateral processes drawn out to equal or exceed the median in length; accessory processes long and acute. *Mouth-parts*: 2nd maxilla bilobed, but without hairy bristles on inner side. Maxillipede with five joints of palp not clearly divided. First *perceopod* with prominent inner process on propodus in male. I find the first three legs of the male to have similar expansions on the carpus and merus to the 1st leg of *L. oceanica*, but Chilton does not mention the point, so it may not be universal or present at all seasons of the year. *Uropods* 17.5 mm.

*Distribution*. "Widely distributed on the warmer shores of the Atlantic, Pacific, and Indian Oceans, and it has been recorded on the American coast as far south as Chili and Puntarenas" (Chilton (1906)). Budde-Lund's specimens are as follows:—Aden; Bagamoja, Shellah-Lama, E. Africa; Bissao; Brazil; Colombo; Malacca; Nagasaki; Rio de Janeiro; Singapore; Pulo Milo, Tonga (Malay Archipelago). (See Richardson (1905) for further list.)

Budde-Lund describes under the name *L. dentipes* a species to which he gives no character that distinguishes it from *exotica*. A careful examination of his specimen reveals no cause why this species should be any longer separated from *L. exotica*.

Figured and described in detail by Chilton (1906).

## 7. *LIGIA OLFERSII* Brandt.

*Ligyda olfersii* Richardson (1905), p. 674 (*q. v.* for synonymy).

Female specimen described, owing to mutilated condition of the males in my possession.

*Length* 19 mm. *Breadth* 9 mm.

*Surface* minutely granular, rather smooth. *Eyes* of narrow-oblong shape, separated by less than their horizontal length. *Antennae* long and slender; flagellum reaching as far back as hind margin of thorax, peduncle to hind margin of 2nd thoracic somite. Flagellum with 26 (broken) long and narrow segments. *Coxal plates* divided by deep grooves on 2nd, 3rd, and 4th thoracic somites. In the male there is no indication of the line of fusion. *Abdomen* not abruptly contracted. *Telson* broadly triangulate; postero-lateral processes acute, but not longer than inner accessory processes; accessory processes strongly marked. *Mouth-parts*: 2nd maxilla weakly bilobed, without hairy bristles; maxillipede, five divisions only indicated on margin and not going right across the palp. *Perceopods* of female typical in form. In the male the carpus and merus of the 1st and 2nd are deeply excavated on the inner side. *Uropods* 11 mm.

*Distribution*. St. Thomas, Trinidad; Florida; Brazil.

Figures in Richardson (1905).

8. *LIGIA ITALICA* Fabricius. (Pl. II. figs. 11 & 12.)*Ligia italica* Budde-Lund (1885), p. 269 (*q. v.* for synonymy).*Ligia italica* Budde-Lund (1908*a*), p. 11.

Male specimen described.

*Length* 8.5 mm. *Breadth* 3.5 mm.

*Surface* nearly smooth; scattered minute granules. *Eyes* of moderate size, somewhat rectangular and separated by horizontal length of one eye or a little less. *Antennæ* long and slender; flagellum reaching as far as hind border of 6th thoracic somite, peduncle to the 2nd. Flagellum with 18-20 long and slender segments. *Coxal plates* either exceedingly faintly separated or the division is apparently obsolete. In the female the separation is marked, but not very distinctly, on the 2nd, 3rd, and 4th thoracic somites. They are but little produced backwards on any somite. *Abdomen* abruptly contracted; lateral margins of somites only very slightly produced backwards. *Telson* arcuate; postero-lateral processes obsolete; only slight undulations mark the accessory processes. *Mouth-parts*: 2nd maxilla strongly bilobed, without hairy bristles; maxillipede with five joints indistinctly separated. *Pereopods* typical in form. *Uropods* 4 mm.

*Distribution*. "A common species on the sea-shore in almost all the countries adjacent to the Mediterranean Sea, also found in the Madeira and Canary Islands" (Budde-Lund (1908*a*)).

I agree with Budde-Lund in looking upon Brandt's *ehrenbergii* as a synonym, but, also with him, I am doubtful of the identity of the specimen described by Dana under that name (1852). The matter is further discussed under *L. gracilipes*.

9. *LIGIA GRACILIPES* Budde-Lund. (Pl. II. figs. 13, 14, & 15.)*Ligia gracilipes* Budde-Lund (1885), p. 270.? *Ligia ehrenbergii* Dana (1852), p. 738.? *Ligia dilatata* Collinge (1920), p. 475.

The somewhat macerated condition of the specimens makes it impossible to give a complete description of any one. The following account applies to the female, and as I cannot be positive that any of the specimens were males, I have not referred to the characters of that sex.

*Length* 7 mm. *Breadth* 3.5 mm.

*Surface* minutely granulated. *Eyes* large and separated by less than their horizontal length. *Antennæ* extraordinarily long and slender. Whole appendage one-quarter as long again as thorax and abdomen together; peduncle reaching as far back as hind border of penultimate *abdominal* somite. Flagellum with 22 (Budde-Lund) very long and slender segments. (A separate antenna had 28 segments; each segment was about five times as long as broad.) *Coxal plates* separated by deep grooves on 2nd, 3rd, and 4th thoracic somites, and distinctly marked on the 5th. *Abdomen* abruptly contracted. *Telson* arcuate; the postero-lateral



processes blunt and but little produced; accessory processes almost obsolete. *Mouth-parts*: 2nd maxilla without any trace of division into two lobes; without hairy bristles on inner side. Maxilliped indistinctly divided into five segments. *Percæopods* very slender, but otherwise typical in form. The *Uropods* were not attached to any specimen, but a separate appendage was 12 mm. in length, the base being 3 mm. and the rami exceedingly long and slender. They are stated by Budde-Lund to be longer than the body.

*Distribution*. S. Africa, "e 'Laudana' exempla pauca in museo Simon asservantur" (Budde-Lund).

Although the material from which this species was made is poor, there is no doubt, I think, that it is a good one. Collinge, (1920), who had only Budde-Lund's short description to guide him, discussing the point, suggests that it is a "young form of some species," admitting, however, that young specimens have, as a rule short antennæ, whereas the *gracilipes* is notable for the great length of the antennæ. He seems to overlook the quite extraordinary length of the uropods. Dana (1852) identified provisionally as *L. ehrenbergii* Brandt, specimens found at Madeira. His description and figures of these specimens apply to *L. gracilipes* in every particular but size and locality. The size he gives as between 17 mm. to 19 mm. long, and 7 mm. to 8 mm. broad—more than double the dimensions of Budde-Lund's specimens. The locality is N.W. Africa as against S. Africa of the *gracilipes*. It seems as if Dana would have been justified in creating a new species for the reception of the specimens, but as he did not do so, they must be identified with *L. gracilipes* if further material should prove them to be the same. I do not think they should be so identified in the present state of our knowledge.

#### 10. *LIGIA HAWAIIENSIS* Dana. (Pl. II. fig. 16.)

*Ligia hawaiiensis* Dana (1852), p. 740.

*Ligia hawaiiensis* Budde-Lund (1885), p. 271.

*Ligia vitiensis* Stebbing (1900), p. 646.

Male specimen described.

Length 19.5 mm. Breadth 7.5 mm.

*Surface* minutely granular. *Eyes* large and quadrangular and separated by less than their horizontal length. *Antennæ* very long and slender; flagellum reaching as far back as hind border of 3rd abdominal somite; peduncle half-way across 3rd thoracic somite; flagellum with 30 long segments, each about twice as long as it is broad. The antennæ in the female reach to the hind border of the thorax, and the flagellum has about 26 segments. *Coxal plates* scarcely, if at all, separated. In the female, deep grooves mark the distinction on the 2nd and 3rd thoracic somites, but indications are absent or exceedingly faint on other somites. *Abdomen* abruptly contracted. *Telson* triangulate; median process



well marked; postero-lateral processes acute but short; accessory processes well marked. *Mouth-parts*: 2nd maxillæ weakly lobed, without hairy bristles on inner side; maxillipede with palp deeply lobed on margin into five portions, but segments otherwise indistinctly marked. First *peræopod* with prominent inner process on propodus in male only. Expansions similar to those of *oceanica* on carpus and merus of this leg. *Uropods* (separate) 7.5 mm.

*Distribution*. Hawaiian Islands; Molokai; Matadona, China Straits, British New Guinea.

I have examined the specimens of the Willey Collection labelled *L. vitiensis*, and identify them, without possible doubt, as this species.

Figured by Dana (1852).

# 11. *LIGIA* *NOVÆ-ZEALANDIÆ* Dana.

*Ligia novi-zealandiæ* Dana (1852), p. 739.

*Ligia cursor* Budde-Lund (1885), p. 265.

*Ligia novæ-zealandiæ* Chilton (1901), p. 106 (*q. v.* for complete synonymy).

*Ligia novæ-zealandiæ* Chilton (1909), p. 287.

*Ligia novæ-zealandiæ* Chilton (1911), p. 568.

Male specimen described.

*Length* 12 mm. *Breadth* 5.5 mm.

*Surface* minutely granular. *Eyes* rather small and quadrangular, and separated by twice their horizontal length. *Antennæ* very long and slender; flagellum reaching as far back as hind border of 4th abdominal somite; peduncle to hind border of 3rd thoracic somite. Flagellum with 20 small and setose segments. The antennæ are shorter in the female. The whole is as long as the thorax, and the peduncle reaches half-way across the 3rd somite. The segments of the flagellum are more setose than in the male. *Coxal plates* very faintly marked or absent. In the female they are marked by deep grooves on the 2nd, 3rd, and 4th thoracic somites. *Abdomen* abruptly contracted. *Telson* arcuate; postero-lateral processes acute and produced, but shorter than middle of hind border; accessory processes marked by slight undulations. *Mouth-parts*: 2nd maxilla with no trace of division into two lobes; without hairy bristles on inner side. *Maxillipede* with 1st and 5th joints only, completely separated, remainder only indicated by indentations on inner side. 1st and 2nd *peræopods* with carpus much swollen in male only; subchelate. *Uropods* 5 mm.

*Distribution*. Coast of New Zealand; Steward Island; Sunday Island, Victoria; Chile; Juan Fernandez.

I found that Budde-Lund's specimens, labelled *Ligia cursor*, from Juan Fernandez (and described by him under that name (1885)) agreed in every particular but length of antennæ with Chilton's description (1901) of *L. novæ-zealandiæ*. These

specimens were all females. An examination of Chilton's original specimens of *novæ-zealandiæ* showed that the antennæ were shorter in the female than in the male, and that the females agreed entirely with Budde-Lund's *cursor*. Fragments of a specimen, labelled "*L. cursor* (male)," from Chile, in Budde-Lund's collection, proved to have subchelate 1st legs like those of the male of the *novæ-zealandiæ*. The *cursor* described by Budde-Lund is therefore synonymous with Dana's *novæ-zealandiæ*.

Dana's original account of *L. cursor* (1852) figures and describes the telson as triangulate. Budde-Lund was misled by the locality of his specimens into crediting Dana with an error on that point, and hence gave a description of *L. novæ-zealandiæ* from S. America (specimens of which he thought he had not seen) under the name of *L. cursor*. The latter species has not apparently been found since Dana described it from "Valparaiso."

The matter is of considerable interest, as Chilton has already had occasion to observe (1909*a* & 1915) the similarity of fauna of South America and New Zealand in connection with other terrestrial and aquatic forms.

Figured and described in detail by Chilton (1901).

12. *LIGIA BAUDINIANA* Milne-Edwards. (Pl. II. figs. 17 & 18.)

*Ligyda baudiniana* Richardson (1905), p. 678 (*q. v.* for synonymy).

Male specimen described.

Length 20 mm. Breadth 9 mm.

Surface rather coarsely granular. Eyes large and separated by less than their horizontal length. Antennæ long and slender; flagellum reaching as far back as hind border of last thoracic somite, peduncle to hind border of 2nd. Antennæ slightly shorter in the female. Flagellum with 29 small and slender segments. Coxal plates very faintly marked on 2nd, 3rd, and 4th thoracic somites. In the female they are very distinct on the corresponding somites. Abdomen not abruptly contracted. Telson triangulate; median process bluntly rounded; posterolateral processes acute, but not projecting as far back as median process; accessory processes represented by undulations. Mouth-parts: 2nd maxilla bilobed, but without hairy bristles on inner side. Maxilliped palp with five distinctly separate segments. Propodus and carpus of 1st *peræopod* (in male only) each produced on inner side to a flat plate-like expansion; free borders each fringed with a comb of exceptionally long and markedly equal setæ. The plates are obliquely striated. Uropods (separate) 12.5 mm. The uropods on the female specimens were shorter in proportion than these, which possibly, however, did not belong to the specimen described above. (In an 18 mm. female the uropods measured 8.5 mm.)

Distribution. Bermudas; Mexico; Yucatan; the Bahamas; Progreso, Colon.

Budde-Lund (1885), without having seen a specimen, regarded this species as a synonym of *L. exotica*. The features which distinguish it from *L. exotica* were fully pointed out by Richardson (1902), with additional evidence for its separation from that species. Chilton (1916), who had not seen a specimen, remarks that it "may be difficult to find characters that will distinguish between them in all cases."

Among Budde-Lund's material, I found a tube bearing a name of an undescribed species of *Ligia* which he evidently intended to describe in the course of his revision of 'Isopoda Terrestria.' An examination of the specimens showed at once that they were identical with Milne-Edwards's *baudiniana*, which had obviously been overlooked by Budde-Lund. This furnishes a further proof of the complete independence of this species from the *exotica*, as upheld by Richardson.

Figures in Richardson (1905).

### 13. *LIGIA* *PIGMENTATA*, sp. n. (Pl. I. figs. 2 & 3.)

The material consisted of a single female specimen and a few appendages which may have belonged to a male.

*Length* 14 mm. *Breadth* 5 mm.

*Surface* slightly granulated, nearly smooth. *Colour* cream, with scattered minute black spots. *Eyes* large, quadrangular and separated by their horizontal length. *Antennae* of moderate length; flagellum reaching as far back as half-way across 5th thoracic somite, peduncle half-way across 2nd somite. Flagellum with 18 short and broad segments. *Coxal plates* with suture lines exceedingly lightly marked on 2nd, 3rd, and 4th thoracic somites only. They are produced but little backwards on any somite. *Abdomen* not abruptly contracted. *Telson* triangulate; median process bluntly pointed; postero-lateral processes acute but short; inner accessory processes small and blunt. *Mouth-parts*: 2nd maxilla strongly bilobed; without hairy bristles on inner edge. Maxillipede palp with joints completely separated. *Pereopods* typical in form. A separate one (male?) had a thick bunch of setae on the dactyl, over the unguis. *Uropods* 6 mm. Base 2.5 mm., rami 3.5 mm.

*Distribution*. Suez.

Budde-Lund had labelled the tube containing this specimen with the above specific name, but had apparently published no description or figures of it.

### 14. *LIGIA* *PERKINSI* (Dollfus). (Pl. I. fig. 1.)

*Geoligia perkinsi* Dollfus (1900), p. 525.

Male specimen described.

*Length* 18 mm. *Breadth* 8 mm.

*Surface* almost smooth. *Eyes* large and separated by their horizontal length or a little less. *Antennae* very long and slender;

flagellum reaching as far back as hind border of 4th abdominal somite; peduncle half-way across 3rd thoracic somite. Flagellum with 30 very long and slender segments. *Coxal plates* show no sign of division from terga, but in the female the sutures are strongly marked on the 2nd, 3rd, and 4th thoracic somites. Hinder thoracic somites and free abdominal somites with postero-lateral angles much drawn backwards and very acute. *Abdomen* not abruptly contracted. *Telson* triangulate; median process blunt; postero-lateral processes acute and drawn out, but not as far back as inner accessory processes. Both accessory processes represented by undulations. *Mouth-parts*: 2nd maxilla weakly bilobed and without hairy bristles. Maxillipede with five separate joints to the palp. *Pereopods* typical in form. *Uropods* 14 mm.

*Distribution*. Hawaiian Islands, Karrai 6000 ft., Oloa 2000 ft.

Although this species is apparently purely terrestrial, it shows no modification whatever from the typical littoral Ligiidæ. The reasons for removing it from Dollfus's genus are given in the beginning of this paper.

#### 15. *LIGIA NATALENSIS* Collinge.

*Ligia natalensis* Collinge (1920), p. 474.

Male specimen described.

*Length* 10 mm. *Breadth* 4.5 mm.

*Surface* minutely granular, rather smooth. *Eyes* moderately large and separated by their horizontal length. *Antennæ* exceedingly long and slender; whole appendage longer than body in male, and as long as body in female; peduncle reaching as far as hind border of 4th thoracic somite in male, and half-way across that somite in female. The flagellum has 20-23 long, slender, and distinctly setose segments. *Coxal plates* show no sign of division from terga, but are faintly marked on 2nd, 3rd, and 4th thoracic somites of female. *Abdomen* abruptly contracted. *Telson* arcuate; postero-lateral processes only very slightly produced; the accessory processes obsolete. *Mouth-parts*: 2nd maxilla not divided into two lobes, without hairy bristles on inner side. Maxillipede with 1st and 5th joints of palp separated; remainder only indicated by deep marginal indentations. *Pereopods* slender, but of typical form. *Uropods*: No specimens of this size had uropods attached. In a male specimen 7 mm. in length they measured 4 mm.; a female 10.5 mm. had uropods of 4 mm.

*Distribution*. Umklali, Winkle Spruit Beach, South Coast, Natal.

This species is nearly related to *L. gracilipes*, but is distinguished from it by the more massive form of body and appendages and the smaller uropods. I am unable to confirm Collinge's observation that the flagella of the antennæ of 7 to 9 mm. specimens of *natalensis* have fewer joints than those of *gracilipes*. In most cases, specimens of that size were as mature in form as larger specimens.

Figured and described by Collinge (1920).

I have not seen specimens of the following species:—

16. *LIGIA DILATATA* Brandt.

*Ligia dilatata* Brandt (1833), p. 171.

*Lygia dilatata* Krauss, Südafrik. Crust., 1843, p. 62.

*Ligia dilatata* White, List Crust. Brit. Mus. 1847, p. 98.

*Ligia dilatata* Budde-Lund (1885), p. 262.

*Ligia dilatata* Stebbing, Ann. South African Mus. 1910, vi. p. 437.

*Ligia dilatata* Collinge (1920), p. 475.

*Distribution.* Cape Peninsula.

Collinge has re-described and figured this species in the last-named work, but has added little to Budde-Lund's previous description. Reasons for regarding *L. glabrata* and *L. gracilipes* as independent species and not as shown in Collinge's synonymy are given above.

17. *LIGIA RICHARDSONÆ* (Pearse).

*Ligyda richardsonæ* Pearse (1915), p. 549.

*Distribution.* Sierra Nevada de Santa Marta, Colombia, at 3800 ft. elevation.

Fully described and figured by Pearse.

18. *LIGIA SIMONI* (Dollfus).

*Geoligia simoni* Dollfus (1893), p. 343.

*Distribution.* Valencia, "vers 1200 mètres d'altitude, dans les forêts."

This species only appears to differ from the preceding in the greater relative breadth of the body and the larger size of the eyes. Dollfus's description is based on a single male specimen, however, and occurring as they do so close together, it is probable that collection of further material will show them to be identical.

Figured and briefly described by Dollfus.

The following species are insufficiently described or of doubtful validity:—

19. *LIGIA CAJENNENSIS* Koch (1847).

20. *LIGIA AUSTRALIENSIS* Dana (1852).

21. *LIGIA CURSOR* Dana (1852).

22. *LIGIA VITIENSIS* Dana (1852).

23. *LIGIA MALLEATA* Pfeffer (1889).

*Distribution* Bagamoyo.

The description of this species and the locality in which it was found suggests its identity with *Ligia exotica*. Pfeffer does not, however, mention the character of the 1st leg nor the sex of the



species he described. If it was a male it differs from *L. exotica* in the absence of a process on the propodus, but if a female it is probably synonymous with *L. exotica*.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. Dorsal view of *Ligia perkinsi*.  $\times 5$ .  
 2. " " *L. pigmentata*, sp. n.  $\times 5$ .  
 3. Telson of *L. pigmentata*, sp. n.  $\times 13.5$ .  
 4. *L. pallasii*. 2nd leg of male.  $\times 5$ .  
 5. *L. glabrata*. Telson and uropods.  $\times 7.7$ .

## PLATE II.

- Fig. 6. *Ligia glabrata*. Antenna.  $\times 9$ .  
 7. *L. occidentalis*. Telson.  $\times 7$ .  
 8. " Antenna.  $\times 6$ .  
 9. *L. cinerascens*. Antenna.  $\times 5$ .  
 10. *L. exotica*. Telson.  $\times 10$ .  
 11. *L. italica*. Antenna.  $\times 7$ .  
 12. " Telson.  $\times 16$ .  
 13. *L. gracilipes*. Antenna.  $\times 7.7$ .  
 14. " Uropod.  $\times 7$ .  
 15. " Telson.  $\times 17$ .  
 16. *L. hawaiiensis*. Telson.  $\times 13$ .  
 17. *L. baudiniana*. Telson.  $\times 11$ .  
 18. " 1st leg of male.  $\times 9$ .



## 36. Monograph of the Hymenopterous Family Stephanidæ.

By ERNEST A. ELLIOTT, F.Z.S., F.E.S.

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(Text-figures 1-8.)

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<i>pygmaeus</i> Enderl. ....	750	<i>tortus</i> Morley ....	731
<i>ruticeps</i> Sauss. ....	737	<i>turcomanorum</i> Semenow. ....	731
<i>rubripes</i> Morley ....	734	<i>unicolor</i> Schlett. ....	725
<i>rustipes</i> Say. ....	716	<i>vadosus</i> Schlett. ....	775
<i>rufofemoratus</i> Szépl. ....	743	<i>villosus</i> Kieff. ....	743
<i>rufo-ornatus</i> Cam. ....	758	<i>violaceipennis</i> Cam. ....	746
<i>rugosus</i> Elliott ....	745	<i>wustnei</i> Schlett. ....	768
<i>salomonis</i> Westw. ....	821	<i>xanthocephalus</i> Cam. ....	724
<i>saussurei</i> Schultz ....	737	XORIDES <i>coronatus</i> Lam. ....	718

## STEPHANIDÆ.

The position of this family remains undetermined, as it appears to form a transition between the Ichneumonidæ and Evanidiæ, with some leanings towards the Braconidæ. Different authors have taken very varied views as to its affinities. Cresson includes only *Stephanus* and the synonymous *Megischus*; Cameron adds *Monomachus*; while Ashmead unites *Stephanus* and *Megalyra*. Even Schletterer, the monographer of the family, declined to express any decided opinion. Some authors unite *Stephanus* and *Stenophasmus* as members of this family, though Ashmead places the latter next to *Doryctes*, and they are now usually considered to be Braconidæ. The two may be easily distinguished:—

Antennæ 30–40-jointed, shorter than body; anterior ocellus surrounded by five frontal tubercles; mandibles recurved, parrot-like; mesonotum not sulcate; scutellum tripartite; posterior femora armed with two or three large teeth beneath. Fore wing with one cubital cell, hind wing without cell, or with one only; abdomen convex beneath.

## STEPHANIDÆ.

Antennæ with about 70 joints, longer than body; frontal tubercles wanting, or not more than two; mandibles not recurved; mesonotum with two longitudinal sulci; scutellum entire; posterior femora mutic; fore wing with two cubital cells; hind wing with two or three complete cells; abdomen more or less concave beneath. . . . STENOPHASMIDÆ.

Roman (Arkiv för zoologi, xi. 1917) states that the structure of the body, especially of the abdomen and legs, is sufficiently characteristic to entitle them to rank as a family, and considers

them to be nearest to the Evaniidæ, especially the Aulacinæ, which have similar habits. Evidence of this is adduced from the general form and the mode of insertion of the antennæ, the tendency of the posterior margin of the head to become collar-like, the strong pleural sulcus for the reception of the middle legs, and possibly also the tendency of the neururation of the wings to become more simple. The special character of the five frontal tubercles occurs in the same manner in the Oryssini, and Roman would place the Stephanidæ as the lowest member of the great group of Ichneumonidæ, between the Evaniidæ and Aculeata.

For convenience, especially as an aid to identification, I accept Enderlein's subfamilies, with the addition of *Neostephanus* Kieffer, while admitting the possibility of transition forms.

Morley (Entom. 1917, p. 106) has drawn attention to the analogy of their structure with that of the Pimplid tribe *Xorides*, to which Lamarck actually ascribed *Stephanus serrator* under the name of *Xorides coronator*.

#### GENERAL DESCRIPTION.

The head is large and globose, with five frontal tubercles surrounding the anterior ocellus, from which the family takes its name (Greek: stephanos, a crown or wreath). The anterior tubercle is frequently larger than the rest, very rarely obsolete; the posterior pair are almost invariably smaller than the others, and have been quite overlooked by some authors, who describe species as trituberculate only.

The powerful mandibles protrude rectangularly, are externally basally angular, anteriorly compressed, pointed and bent downwards like the beak of a parrot, with long grey to golden pubescence beneath. The maxillary palpi are long, slender, and five-jointed; basal joint short, second twice as long as first, the others of about equal length. The labial palpi are short and four-jointed; the three basal joints clavate, the apical cylindrical and longer. The eyes are large and roundish elliptical. Straight lines joining the ocelli would form an equilateral triangle with the base behind; the posterior ocelli are close to the interior margin of the eyes. The 30-40-jointed antennæ are placed very low down, the face being very short, cheeks normally as long as scape, and the frons proportionately large. Temples usually smooth and shining. The scape is incrassate, and the other joints, especially towards the middle, indistinctly discreted, gradually shorter and more slender towards the apex, distinctly pubescent except the basal ones; second flagellar joint normally twice as long as first; third as long as first and second together.

The frons is more or less coarsely arcuately, transversely, or irregularly striate; the occiput has usually several transcarinæ close to the posterior tubercles, posteriorly often transversely rugose and laterally irregularly punctate rugose. Temples

usually polished smooth, with a few scattered punctures, rarely distinctly rugose. The cheeks are always distinctly developed and usually about the same length as the scape. The posterior margin of the head is either simple (*serrator*), bordered (*furcatus*), or produced into a more or less distinct collar (*collarifer*).

The pronotum consists of an anterior narrowed neck, which is usually more or less distinctly transrugose, and a posterior crescentic part—herein called the semiannular—which is either entirely smooth or more or less finely rugose, with a narrow polished posterior margin. The mesonotum is curvate in front, rugose or punctate, rarely smooth; it has a central longitudinal row of punctures, sometimes almost obsolete, on each side of which is a smooth space, beyond which are two lateral impressions or rows of punctures. The scutellum is divided into three sections by distinct crenulate sulci, is almost smooth, with a few large punctures on the margins of the lobes, of which the lateral ones are often more or less punctate. The mesopleuræ are deeply impressed above, somewhat smooth and shining, distinctly sculptured below. The metapleuræ are often separated from the median segment by a row of punctures, a sulcus or a carina, or rarely by a sulcus and a carina; less commonly confluent. Of the metanotum proper only a very narrow band, laterally broader triangular, is seen and is longitudinally striate. The median segment is large, usually with large, shallow punctures; sometimes the interstices are alutaceous, and rarely, as in *gigas*, it is rugose, anteriorly often diffusely punctate, and more or less grey pubescent. The abdomen is inserted near the apex of the median segment, not far from the hind coxæ. The petiole is rarely sessile, as in *Schlettererius*, usually nearly as long as the remaining segments together; it is very rarely smooth (*maculipennis*), usually more or less finely trans-striate. The remainder of the abdomen is usually smooth, with a few dull spots, due to microscopic sculpture, more rarely entirely dull. There are seven segments in the male, six in the female, the posterior ones being short and indistinctly discreted. The terebra in female is usually as long as or longer than the whole body, the spicula ferruginous or red, its sheaths entirely black, or white or pale-banded before the apex, rarely rust-red (*insignis*).

The anterior legs are short, their femora and tibiæ comparatively slender, the tarsi five-jointed, the penultimate joint very short and furnished with pencils of hair. The hind legs are very elongate, their coxæ stout, usually transrugose, often with finer striation between coarse transverse ridges. The second joint of the trochanters is indistinct. The hind femora are strongly fusiform, smooth and polished, rarely finely sculptured; on the under side they bear two or three large teeth and a varying number of smaller serrations. The hind tibiæ are compressed either in the basal third, or as far as, or even beyond, the middle and constricted. The hind tarsi are usually five-jointed in the

male and three-jointed in the female; only in *Schlettererius* and *Stephanus serrator* they are five-jointed in the female and three-jointed only in *S. tibiator* male.

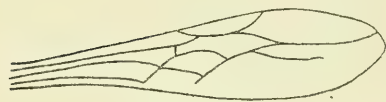
## Text-figure 1.

*Stephanus.*

1. Neurulation complete.

*Parastephanellus.*

2. Discoidal cell  $\frac{1}{4}-\frac{1}{3}$  of cubital cell, not touching the submedian, and more or less petiolate. External submedian cell open behind. Radius not extending to margin of wing.

*Hemistephanus.*

3. Discoidal cell about as large as cubital, touching submedian cell. External submedian cell open behind. Radius extends to margin of wing.

*Neostephanus.*

4. Cubital and discoidal cells wanting; external submedian cell open behind.

*Foenatopus.*

5. External submedian cell is indicated by a part of the median nervure only.

*Diastephanus.*

6. External submedian cell entirely wanting.

The neurulation of the wings shows five, apparently constant forms, which have been utilized as the foundation of as many subgenera.



Schultz (Spolia Hymenop. 1906, p. 273) writes: "I cannot accept *Fœnatopus* Sm. or any of the newly-erected genera of *Stephanus* Jur., as they are purely artificial, and useful at most for distinguishing groups of species in this rich genus." Are not most of our genera artificial, and is not their object exactly that stated above? Cameron, again, in Ann. Soc. Ent. Belg. lvi. 1912, p. 358, makes the curious statement: "There are three longitudinal nervures, which is one of the points separating *Stephanus* from *Parastephanus*." There are always three such nervures, the difference being in the development.

When the neururation is complete, as in *Stephanus*, s. str., there are three basal cells: costal, which is very narrow and often indistinct, median and inner submedian; an outer series of three: cubital, discoidal, and external submedian; and a long, somewhat narrow radial cell. The type of this subgenus is *Stephanus serrator* Fab.

In the second form the neururation is similar to that of the second, but the discoidal cell is only about one-fourth of the size of the cubital, and is petiolate, not touching the inner submedian. They are Indo-Australian. Type: *Parastephanellus pygmaeus* Enderl.

In the third form the submedian or posterior nervure is abbreviated, not extending beyond the apex of the inner submedian cell; the external submedian cell is thus open behind. The discoidal cell is about the same size as the cubital, and touches the inner submedian cell on a longer or shorter base. This subgenus, *Hemistephanus* Enderl., is exclusively Neotropical. The type is *H. macrurus* Schlett.

In these three subgenera the stigma is opaque and the bounding nervures indistinct. In the three following subgenera the stigma is smaller, translucent, the bounding nervures distinct, the cubital and discoidal cells wanting.

In the fourth form, *Neostephanus* Kieff., there are three complete basal cells; the median nervure extends to the full length of the outer submedian cell and the second transverse nervure is present, the outer submedian cell being thus bounded on three sides. Type: *Neost. alluaudi* Kieff.

Form five, *Fœnatopus* Smith, differs in having only a short prolongation of the median nervure beyond the basal cells, without any indication of the second transverse nervure. Type: *F. indicus* Westw.

Form six, *Diastephanus* Enderl., has the neururation still further reduced, no nervure extending beyond the basal cells. Type: *D. flavomaculatus* Enderl.

In these three forms the radius does not extend to the margin of the forewing, the radial cell being apically incomplete.

The colour in the majority of species is mainly black, frequently inclining to brownish; the head is often ferruginous or red, antennæ and mandibles basally and the legs more or less red.



A few species are fulvous, as *F. natalicus* Westw. The size varies enormously within the same species, e. g. *S. coronator*, 20–40 mm. The terebra in female varies greatly in different species, but appears to retain the same proportional length in each species. The males are, as a rule, smaller and more slender than the females, although individuals may exceed the size of the smaller females.

Very little appears to be known as to the life-history of these insects. Jurine writes of *S. serrator* as living in dry wood; Montrouzier observed *S. hæmatipoda* flying from trunk to trunk on the edge of a wood; the Cuban *S. brunneus* was taken in some numbers and in both sexes coming out of the same hole in a diseased tree, called Jalia. Roman (Arkiv för zoologi, 1917) considers it to be certain that they are forest insects and parasites on wood-boring larvæ. He found them always round fallen or dead trees, which were infested by the larvæ of Rhyncophora, Anthribidæ, Longicornia, and Buprestidæ. He hazards a conjecture that the special hosts belong to the Brentidæ, which, like the Stephanide, are slender, elongate creatures, occurring in all warm countries.

There can be little doubt that the family is more widely distributed and the individuals more numerous than at present supposed. No collector had paid special attention to them till Roman did so in 1914–15 in Brazil, where he took 98 specimens, representing 7 species, all belonging to the subgenus *Hemistephanus*. It is somewhat remarkable that *H. vadosus* accounts for 68 specimens, and that his two new species, *H. angulicollis* and *glabricoxis*, are represented each by one female only. The formation of the prothorax in these is very characteristic.

One difficulty, inseparable from every attempt to compile a monograph without having access to authenticated specimens of every species, lies in the fact that every author has his own methods of description, and lays especial stress on different characters. Schletterer first gave scientific descriptions, including details of the posterior margin of the head, proportions of the basal flagellar joints, relative length of petiole to the remaining segments, and general sculpture.

Enderlein desires to emphasize the value of the microscopic sculpture of the central tergites, while Roman finds in the sculpture of the pronotum valuable characters for the determination of species.

Smith and Cameron have given us many quite worthless descriptions, based largely on colour only, but worst of all are Westwood's notes, one cannot call them descriptions, of *S. diadema* and *frontalis* in the Trans. Ent. Soc. Lond.

What may be the effect of the Great War on the various collections, especially in Belgium, cannot yet be known, but it is certain that the German lust of destruction has caused heavy loss to science in all non-militant branches.

*Table of Genera.*

- |       |                                                                                                                                                       |                              |
|-------|-------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------|
| (2.)  | 1. Hind wing with basal cell; abdomen sessile.....                                                                                                    | 1. <i>Schlettererius</i> .   |
| (1.)  | 2. Hind wing without basal cell; abdomen petiolate.                                                                                                   |                              |
| (8.)  | 3. Cubital and discoidal cells present; stigma thick, chitinated;<br>the bounding nervures indistinct .....                                           | (STEPHANINÆ.)                |
| (5.)  | 4. Neuration complete .....                                                                                                                           | 2. <i>Stephanus</i> .        |
| (4.)  | 5. Median vein incomplete, outer submedian cell open behind.                                                                                          |                              |
| (7.)  | 6. Discoidal cell about $\frac{1}{2}$ of the size of the cubital cell, does not<br>touch the submedian cell, but is petiolate; stigma broad.          | 3. <i>Parastephanellus</i> . |
| (6.)  | 7. Discoidal cell nearly as large as the cubital, and touches the<br>submedian on a longer or shorter base; stigma narrow,<br>long, and pointed ..... | 4. <i>Hemistephanus</i> .    |
| (3.)  | 8. Cubital and discoidal cells wanting; stigma hyaline, bounding<br>nervures distinct .....                                                           | (FENATOPODINÆ.)              |
| (12.) | 9. External submedian cell present partly.                                                                                                            |                              |
| (11.) | 10. " " " open behind only .....                                                                                                                      | 5. <i>Neostephanus</i> .     |
| (10.) | 11. " " " open apically and behind.                                                                                                                   | 6. <i>Fenatopus</i> .        |
| (9.)  | 12. " " " entirely wanting .....                                                                                                                      | 7. <i>Diastephanus</i> .     |

SCHLETTERERIUS Ashm.

*Schlettererius* Ashmead, p. 150; *Stephanus* Say, p. 61; Cresson (2), 1880, p. xviii.

This genus appears to agree with *Stephanus* Jur. in the venuration of the fore wings, the formation of the mandibles and the insertion of the antennæ, but differs in having one complete cell in hind wing, abdomen sessile, the basal segment being not, or but little, longer than the second.

Only one species, *S. cinctipes* Cress., has hitherto been recognized, but the description of *S. rufipes* Say, though defective, suffices to place it here. I give the original descriptions.

1. RUFIPES Say, *l. c.*

*Stephanus Jur.*

"*S. rufipes*. Black; abdomen sessile; thorax not remarkably attenuate before. Inhabits Pennsylvania.

“Body somewhat sericeous; palpi pale yellowish; scutellum with a groove on each side, rough; metathorax rough, and with two slightly elevated longitudinal distant lines; wings hyaline; a large triangular fuscous carpal spot; feet rufous; posterior pair of tarsi dusky; abdomen a little rough at base; oviduct as long as abdomen.

“Length one-fifth of an inch.

"Although the arrangement of the wing nervures agrees precisely with *S. coronatus* Jur., yet the form of the body differs materially, the thorax not exhibiting the remarkable attenuation before, and the abdominal petiole is not visible."

## 2. CINCTIPES Cress.

*Stephanus cinctipes* Cress. (2), p. xviii; Schlett., p. 156. *Schlettererius*, Ashm., l. c.

"♀. Black; labrum, narrow band at base of all the tibiæ, and apical third, except extreme tip of the ovipositor sheaths, white; tarsi testaceous, paler at base; trochanters, apex of first abdominal segment above, and most of the second and third segments, ferruginous; in front of ocelli a sharp semicircular carina, toothed in the middle and on each side; face transversely rugose; cheeks nearly smooth; immediately back of ocelli a series of sharp transverse ridges (sometimes this part is tinged with dull ferruginous); mesothorax finely, transversely wrinkled, the impressed longitudinal lines composed of deep pits; pleuræ and metathorax roughly punctured, the former less so and shining; middle of scutellum smooth and polished; tegulæ dull testaceous; wings pale fuscous towards tips, an angular subhyaline band commencing at base of stigma, apex of wings paler than beneath stigma; all tarsi 5-jointed, the penultimate joint with a long tufted process at the tip beneath; anterior tarsi double the length of their tibiæ and very slender; posterior coxæ large and toothed above near the apex, their femora with two large teeth beneath, and a number of small unequal teeth between and on either side of them; their tibiæ not much thickened toward tip and not dilated; their tarsi about two-thirds the length of the tibiæ, with the first joint rather longer than the second, which is about equal in length with the third; abdomen smooth and polished, except the first segment, which is finely roughened and not longer than the posterior coxæ; ovipositor about double the length of the body. Length .55-.75 inch."

Habitat: Washington Territory (Morrison).

Schletterer (*l. c.*) gives the habitat as "Subreg. 3. United States, Massachusetts, Pennsylvania, Washington, New York," and adds that *S. cinctipes* is connected with the European *S. serrator* by its 5-jointed hind tarsi, and partly by the style of its sculpture, but differs in having two large teeth on the hind femora (*serrator* has three), in the sheaths of the terebra being white-banded before the apex, etc.

Ashmead (*l. c.*) says: "Posterior tarsi in both sexes normal, unarmed." This appears to be a misprint for "femora," and is incorrect since *cinctipes* has the hind femora armed with two large teeth beneath.

*S. coronatus* Panz., Jur., etc. is a synonym of *S. serrator* Fab. The two species differ in size, colour, and especially in the relative length of terebra; both occur in Pennsylvania.

Say (*l. c.*) states that the neururation of his *rufipes* agrees precisely with that of *S. coronatus* Jur., but does not especially mention the basal cell in hind wing.

## STEPHANUS.

The designation *Stephanus* Jur., originally applied to the whole family, was restricted by Enderlein (2), p. 473, to the species possessing "complete" neurulation, comprising three basal cells, the costal, median and inner submedian, and three outer cells, cubital, discoidal, and external or outer submedian, together with a closed radial cell; and I follow him in calling this group, so characterized, the subgenus *Stephanus*.

Unlike other subgenera, it is distributed throughout the whole range of the family, and to it belong the few known European species.

There does not appear to be any character, other than the neurulation, by which the species of this subgenus can be distinguished from those of any other. As a rule they are large insects, mainly black, often with a red head, but size varies in the females from 10-40 mm.

The terebra varies from slightly shorter than the body to twice its length. The males are mostly smaller than the females, though in some species the few specimens known of both sexes are nearly of the same size. Temples smooth and shining, unless otherwise stated.

The type of the subgenus is *S. serrator* Fab., which is unfortunate in some respects, as it has five-jointed hind tarsi in both sexes and tridentate femora; the former character is unique and the latter is shared only by *S. borneensis* Sauss. *S. tibiator* Schlett., from Aden, is exceptional in having the hind tarsi three-jointed in the male.

The characters utilized for differentiation of species in the following table are: 1st, number of joints in hind tarsi; 2nd, sculpture of temples; 3rd, colour of sheaths of terebra. Other important points are: relative proportion of petiole to rest of abdomen; sculpture of head and thorax; length of basal antennal joints: and colour of wings.

The colour of the head (black, red, or, in one case, yellow) is a good distinction; here, as among Coleoptera, it is often found the black shows a tendency to become rufescent, but can never be mistaken for a true red.

*Table of Species.*

♀.

- |      |                                                                                                      |                              |
|------|------------------------------------------------------------------------------------------------------|------------------------------|
| (2.) | 1. Hind tarsi 5-jointed; hind femora tridentate; temples finely rugose-punctate. 8-17 mm. ....       | 1. <i>serrator</i> Fab.      |
| (1.) | 2. Hind tarsi 3-jointed; hind femora bidentate (except No. 25).                                      |                              |
| (8.) | 3. Temples coarsely rugose-punctate.                                                                 |                              |
| (5.) | 4. Antennæ very short; temples with a smooth space behind eyes; head bordered; mesonotum entire..... | 2. <i>antinorii</i> Gribodo. |
| (4.) | 5. Antennæ normal.                                                                                   |                              |
| (7.) | 6. Temples with smooth raised space behind eyes; prothorax normal; hind femora slender.....          | 3. <i>gigas</i> Schlett.     |



- (6.) 7. Temples without smooth space behind eyes; prothorax with an inflated ring between neck and semiannular; hind femora very incrassate..... 4. *tibiator* Schlett.
- (3.) 8. Temples smooth.
- (22.) 9. Sheaths of terebra entirely black.
- (11.) 10. Frons coriaceo-granulate, legs entirely smooth ... 5. *nigricauda* Sichel.
- (10.) 11. Frons arcuate or trans-rugose, legs distinctly sculptured.
- (15.) 12. Frons arcuate rugose.
- (14.) 13. Petiole shorter than rest of abdomen; terebra about one-third longer than body; head red ..... [Schlett. 6. *pachylomerus*
- (13.) 14. Petiole longer than rest of abdomen; terebra half as long again as body; head pale yellow, black banded. [Cam. 7. *xanthocephalus*
- (12.) 15. Frons coarsely, irregularly, or transversely rugose.
- (17.) 16. A distinct sulcus across vertex and part of occiput; terebra nearly half as long again as body; wings infumate, centrally darker ..... 8. *sulcifrons* Schlett.
- (16.) 17. No distinct sulcus on head or occiput.
- (19.) 18. Dark chestnut-brown; sheaths of terebra blue-black. 9. *brunneus* Cam.
- (18.) 19. Head black; body chiefly black.
- (21.) 20. Petiole and hind coxæ coarsely transrugose; wings infusate. 10. *unicolor* Schlett.
- (20.) 21. Petiole finely trans-striate; hind coxæ smooth; wings subhyaline, iridescent ..... 11. *hornianus* Enderl.
- (9.) 22. Sheaths of terebra white-banded before apex.
- (42.) 23. Posterior margin of head simple, not bordered or reflexed.
- (33.) 24. Terebra about as long as body.
- (30.) 25. Head black.
- (29.) 26. Second flagellar joint twice as long as first, third little shorter than first and second together.
- (28.) 27. Mesonotum confluent punctate; hind femora shining, smooth ..... 12. *andinus* Schlett.
- (27.) 28. Mesonotum irregularly rugose-punctate; hind femora dull. 13. *sickmanni* Schlett.
- (26.) 29. Second and third flagellar joints of equal length and little longer than first..... 14. *crassicauda* Morley.
- (25.) 30. Head not black.
- (32.) 31. Head, anterior femora and tibiæ mostly, and all tarsi red. 15. *tarsatus* Sichel.
- (31.) 32. Head yellow, body dull ferruginous ..... 16. *texanus* Cress.
- (24.) 33. Terebra distinctly longer than body.
- (35.) 34. Petiole basally smooth, head granulate, mesonotum coriaceo-punctate ..... 17. *europæus* Sichel.
- (34.) 35. Petiole basally striate, head and mesonotum otherwise sculptured.
- (37.) 36. Mesonotum smooth, 2nd and 3rd flagellar joints of equal length and little longer than first ..... 18. *tortus* Morley.
- (36.) 37. Mesonotum more or less punctate.
- (41.) 38. Mesonotum rugose-punctate.
- (40.) 39. Median segment centrally densely punctate, laterally diffusely. Head and thorax black, abdomen brown, petiole rufescent. 19. *anomalipes* Fst.
- (39.) 40. Median segment evenly rugose-punctate throughout. Head and thorax ferruginous, abdomen red-brown, petiole nigrescent ..... 20. *bicolor* Westw.
- (38.) 41. Mesonotum diffusely punctate, median segment coarsely reticulate ..... 21. *nigricans* (Sichel).
- (23.) 42. Posterior margin of head bordered or reflexed.
- (60.) 43. Posterior margin of head bordered but not reflexed.



- (49.) 44. Terebra about as long as or very little longer than body.  
 (46.) 45. Petiole much shorter than rest of abdomen, mesonotum finely trans-striate and diffusely punctate ..... 22. *niger* Smith.  
 (45.) 46. Petiole as long as or very slightly shorter than rest of abdomen, mesonotum not trans-striate.  
 (48.) 47. Wings brown, centrally darker ..... 23. *froggatti* Cam.  
 (47.) 48. Fore wings hyaline, with steely iridescence ..... 24. *ceylonicus* Cam.  
 (44.) 49. Terebra distinctly longer than body.  
 (51.) 50. Hind femora tridentate, forewings fuscous, with darker spot or fascia in middle ..... 25. *borneensis* Sauss.  
 (51.) 51. Hind femora bidentate.  
 (55.) 52. Wings evenly infumate.  
 (54.) 53. Frons arcuate rugose; metapleuræ coriaceous above, diffusely punctate beneath; entirely black or black-brown. 26. *furcatus* Lep. & Serv.  
 (53.) 54. Frons irregularly rugose, metapleuræ densely punctate, head red ..... 27. *ruficeps* Sauss.  
 (52.) 55. Wings centrally or distally darker.  
 (59.) 56. Wings centrally darker, petiole shorter than rest of abdomen.  
 (58.) 57. Head not impressed behind vertex, semiannular smooth, mesonotum posteriorly confluent punctate ... 28. *coronator* Fab.  
 (57.) 58. Head compressed behind vertex, semiannular transrugose, mesonotum posteriorly coarsely transrugose ... 29. *ducalis* Westw.  
 (56.) 59. Wings infumate, external median and submedian cells and then to margin of wing dark brown, petiole as long as rest of abdomen ..... 30. *lanceolatus* Kieff.  
 (43.) 60. Posterior margin of head reflexed, collar-like.  
 (62.) 61. Wings strongly infumate, centrally darker; petiole shorter than rest of abdomen ..... 31. *hæmatipoda* [Montrz.  
 (61.) 62. Wings slightly infusate or hyaline, petiole as long as rest of abdomen.  
 (64.) 63. Head black, cheeks pale marked, median segment cribrate punctate ..... 32. *acutus* Lep. & Serv.  
 (63.) 64. Head red, median segment confluent punctate. 33. *villosus* Kieff.

## ♂.

- (2.) 1. Hind tarsi 3-jointed, hind femora bidentate ..... 4. *tibiator* Schlett.  
 (1.) 2. Hind tarsi 5-jointed.  
 (6.) 3. Hind femora tridentate.  
 (5.) 4. Mesonotum irregularly rugose, metapleuræ rugose; wings hyaline, centrally and apically infusate ..... 1. *serrator* Fab.  
 (4.) 5. Mesonotum cribrate punctate, metapleuræ densely punctate; fore wings with transverse dark band ..... 25. *borneensis* Sauss.  
 (3.) 6. Hind femora bidentate.  
 (10.) 7. Posterior margin of head produced, collar-like.  
 (9.) 8. Posterior margin of head translucent but not reflexed. Metapleuræ and median segment partly confluent punctate. 33. *villosus* Kieff.  
 (8.) 9. Posterior margin of head reflexed. Lateral lobes of scutellum coarsely punctate; metapleuræ and median segment not confluent punctate ..... 36. *pilosus* Elliott.  
 (7.) 10. Posterior margin of head bordered, but not collar-like.  
 (12.) 11. Wings subhyaline green and red iridescent; outer orbits are white-marked ..... 11. *hornianus* Enderl.  
 (11.) 12. Wings not iridescent.  
 (20.) 13. Wings infumate, centrally darker.  
 (17.) 14. Head red.

- (16.) 15. Head impressed behind vertex; semiannular transrugose; mesonotum centrally smooth, metapleuræ coarsely rugose. 29. *ducalis* Westw.
- (15.) 16. Head not impressed behind vertex; semiannular smooth; mesonotum densely, partly confluent punctate; metapleuræ densely punctate. 28. *coronator* Fab.
- (14.) 17. Head black.
- (19.) 18. Second and third flagellar joints of equal length and little longer than first; median segment densely punctate; petiole shorter than rest of abdomen, trans-striate throughout. 23. *rubripes* Morley.
- (18.) 19. Second flagellar joint twice as long as first, third distinctly longer than second; median segment diffusely punctate; petiole smooth, only basally rugose. 34. *rufofemoratus* [Szépl.]
- (13.) 20. Wings not centrally darker.
- (28.) 21. Wings more or less infumate.
- (25.) 22. Thorax confluent punctate.
- (24.) 23. Petiole trans-striate, rest of abdomen smooth and shining. Dark chestnut-brown. 9. *brunneus* Cress.
- (23.) 24. Petiole very finely transaciculate, rest of abdomen finely alutaceous. Black; head and anterior legs red. 35. *comma* Morley.
- (22.) 25. Thorax otherwise sculptured.
- (27.) 26. Vertex transrugose; median segment scrobiculate reticulate; hind coxæ trans-striate. Black; head red. 15. *tarsatus* Sichel.
- (26.) 27. Vertex arcuate striate; median segment densely, partly confluent punctate; hind coxæ finely striate between coarse scale-like rugosities. Black to dark brown, cheeks white-marked. 26. *furcatus* Lep. & [Serv.]
- (21.) 28. Wings clear hyaline; vertex and occiput longitudinally carinate. 37. *rugosus* Elliott.

### 1. SERRATOR Fab.

*Ichneumon* No. 193, Zschah, i. p. 60, ♀; tab. *Synistata*, fig. 193, ♀, 1789. *Ichneumon serrator* Fab. (1), p. 224, ♀, 1798. *Stephanus coronatus* Panz., pl. et fig. 13, 1801, ♀; Jur., tab. 7, ♀; Lep. & Serv., p. 489, pl. 376, fig. 2 a, b, c, ♀; Nees ab Es., i. p. 8, 1834, ♀; Blanch., p. 23. *Bracon serrator* Fab. (2), p. 108, ♀. *Ichneumon coronatus* Latr., p. 179, ♀. *Xorides coronatus* Lamarck, p. 135; l. c. iv. Ed. 2, 1835, p. 347. *Stephanus serrator* Brull., p. 537, ♀; Westw. (4), p. 227, ♀; Sichel (2), p. 472, ♀ ♂; Schlett., p. 91, ♀ ♂; André, p. 481, ♀ ♂.

♀ ♂. Head with frons moderately coarsely and regularly, occiput more finely and irregularly rugose, arcuately near the posterior ocelli. Temples finely rugose-punctate, with a small smooth raised space behind eyes. Posterior margin of head simple. Second flagellar joint twice as long as first, third longer than second, but shorter than first and second together. Neck coarsely transrugose, semiannular more finely. Mesonotum coarsely and irregularly rugose, more finely to nearly smooth in front, with a distinct central longitudinal channel and two lateral divergent rows of small punctures. Mesopleuræ coriaceous rugose, with coarser reticulations behind; scutellum centrally smooth, laterally longitudinally rugose; metapleuræ rugose, but less coarsely than the median segment, from which they are

separated by a distinct sulcus. Petiole stout, irregularly rugose, basally more coarsely, much shorter than the remaining feebly shining part of abdomen. Terebra longer than body, its sheaths entirely black. Hind legs with the coxæ finely coriaceous; femora tridentate, tibiæ constricted beyond middle and longer than femora; hind tarsi five-jointed in both sexes.

Black; antennæ basally brown; mandibles basally ferruginous, cheeks white-marked; abdomen rufescent, apically black, or entirely black; legs brown, rufescent beneath, their joints whitish. Wings basally hyaline, centrally and apically slightly infusate.

Length 8-17 mm.

Habitat: Germany, France, and Central Europe.

The tridentate hind femora and five-jointed hind tarsi will suffice to distinguish this species ♀, and the only other ♂ with the former character (*borneensis* Sauss.) is nearly twice as large.

## 2. ANTINORII Grib.

*Megischus antinorii* Gribodo, p. 346, ♀. *Stephanus ant.* Schlett., p. 108; W. A. Schulz (2), p. 16, ♀.

♀. Frons moderately shining, densely and irregularly, not arcuately, reticulate rugose. Five frontal tubercles (not six as stated by Gribodo in his original description), of nearly equal size, a triangular space in front of the anterior ocellus shining smooth. Vertex densely, coarsely, and deeply rugose-punctate, with five curved carinæ in front and a longitudinal impression behind. Occiput coarsely but diffusely and not deeply rugose-punctate, without longitudinal impression. Posterior margin of head sharply bordered. Cheeks rather shorter than scape and as long as second flagellar joint, shining smooth and diffusely punctate. Temples with a smooth shining protuberance near eyes (as in *gigas*), above it coarsely and deeply punctate, below densely and coarsely rugose-punctate. Antennæ unusually short, 32-jointed, reaching only to the base of median segment; second flagellar joint two and a half times as long as first, third only as long as second. Neck weakly transrugose, separated by a right-angled impression from the semiannular, which is densely and coarsely rugose-punctate, with a broad smooth posterior margin. Prosternum shining, anterior third finely rugose-punctate, remainder smooth with very sparse and deep punctures. Mesonotum entire, centrally almost smooth, otherwise very coarsely, but not deeply or densely rugose-punctate. Scutellum shining, with a few punctures on the lateral lobes, and the borders of central lobe finely striated. Mesopleuræ densely and coarsely reticulate, with a smooth shining space below tegulæ and above middle coxæ. Metapleuræ prominent, coarsely reticulate rugose, with a broad, deep, and curvately carinate impression in front and a similar smoother impression behind. Median segment discally extremely coarsely reticulate, laterally rugose, separated from

the metapleuræ by a fine longitudinal carina, behind which is a narrow sulcus. Petiole basally transrugose, then finely trans-striate, apically smooth, shorter than rest of abdomen. Terebra nearly as long as body, ferruginous, sheaths entirely black. Hind legs with coxæ stout, with setiferous punctures in front, more sparse towards middle, apically finely trans-striate; femora inflated, microscopically finely and densely alutaceous and punctate.

Head, thorax laterally, legs including tibiæ and petiole beneath with long, sparse, coarse hairs; similar but shorter and finer hairs on abdomen.

Wings hyaline, apically infumate, stigma opaque, nervures pitch-brown.

Black; mandibles and antennæ red-brown; cheeks and base of anterior femora red-yellow. Wings faintly iridescent.

Length 25 mm. Terebra 23 mm. (Gribodo: 26 mm.; terebra 20 mm.)

Habitat: Mahal Uonz, Shoa, East Africa, 1 ♀ taken by Marquis Orazio Antinori. Described from the unique type in the Museum at Genoa by W. A. Schulz.

The extremely short antennæ and six frontal tubercles, as described by Gribodo, inclined Schletterer to doubt this species being a true *Stephanus*, but the latter character proves to be a mistake, the five frontal tubercles being quite normal; and Schulz states that the right antenna is complete, the apical joint is normally pointed and  $1\frac{1}{2}$  times as long as the penultimate, not showing any signs of being abnormally formed or dwarfed.

This species resembles *S. gigas* and *S. tibiator* Schlett. in the very coarse sculpture of the body and especially of the temples, but differs from both in the unusually short antennæ. From *S. gigas* it may be further distinguished by the bordered posterior margin of the head and by the broadly smooth posterior margin of prothorax; from *S. tibiator* it differs in the absence of the longitudinal sulcus on occiput, in the formation and sculpture of the prothorax, etc. No other specimen having been yet taken, it must remain uncertain whether the short antennæ are truly characteristic of the species.

### 3. GIGAS Schlett.

*Stephanus gigas* Schlett., p. 96.

Frons very coarsely and irregularly rugose; occiput arcuately rugose near the posterior ocelli, behind this centrally transversely, laterally irregularly rugose. Temples covered with dense, rather deep and partly confluent punctures, excepting a smooth space behind ocelli. Posterior margin of head simple. Second flagellar joint fully twice as long as first, third only as long as second. Neck coarsely transrugose, semiannular coarsely rugose-punctate throughout, excepting an indistinctly rugose impression near tegulæ. Mesonotum centrally somewhat smooth,



with a central longitudinal row of broad and deep punctures, and two deep, divergent sulci, laterally very coarsely rugose-punctate. Central section of scutellum smooth, with a few marginal punctures; lateral lobes densely, coarsely, and partly confluent punctate. Metapleuræ and median segment very coarsely and reticulately rugose, separated by a deep rugose sulcus. Hind legs with the coxæ short and stout, transrugose, more finely behind; femora comparatively small and slender, polished smooth, with two large teeth; tibiæ much longer than femora and compressed only in basal third.

Black; mandibles basally and hind coxæ ferruginous, antennæ with basal half brownish.

Habitat: Schiras, Persia. Type in Imp. Nat. Hist. Museum, Vienna.

This description was taken from a specimen without abdomen, and as no mention is made as to the number of hind tarsal joints, the sex cannot be determined. It appears to resemble closely *S. tibiator* Schlett. from Aden, in the coarse sculpture of head and temples, though differing in the structure of pronotum and in the slender hind femora.

#### 4. *TIBIATOR* Schlett.

*Stephanus tibiator* Schlett., p. 293, ♀ ♂; Morley (1), pp. 34 & 112, ♀.

♀ ♂. Frons very coarsely and irregularly to reticulately rugose; vertex obliquely arcuate rugose; occiput very irregularly punctato-rugose, with a central longitudinal impression. Temples coarsely and deeply punctate, posteriorly more diffusely and cleanly, near the cheeks more densely and confluent. Cheeks feebly punctato-rugose. Second flagellar joint twice as long as first, third slightly more slender than second and but little longer. Neck very short, laterally coarsely rugose, above with two large foveæ separated by a longitudinal carina; then follows a coarsely rugose-punctate inflated part, separated by a distinct constriction from the semiannular, which is apically coarsely rugose, centrally and laterally densely and partly confluent punctate, with a polished smooth posterior margin. Mesonotum centrally diffusely punctate, apically and laterally rugose; scutellum smooth with diffuse punctures, its three lobes defined by crenulated sulci. Mesopleuræ rather coarsely and irregularly rugose in the upper impressed part, irregularly to reticulately rugose beneath, with a smooth, shining, and diffusely punctate space near the tegulæ; metapleuræ very prominent, coarsely and irregularly rugose, separated by a deep sulcus from the coarsely reticulate rugose median segment. Petiole trans-striate, apically smooth and shining. Terebra shorter than body, sheaths entirely black. Hind legs with coxæ basally densely aciculate punctate, apically transrugose; femora strikingly



incrassate, bidentate, smooth and shining, with diffuse setiferous punctures; tibiæ as long as femora, compressed to about middle; tarsi three-jointed in both sexes.

Black, with a tendency to brownish, especially in the cheeks and tarsi. Antennæ ferruginous in ♀, black in ♂. Wings hyaline.

In ♂ the rugosity of the semiannular is more pronounced than the puncturation; the lateral lobes of the scutellum are more rugose than punctate; the abdomen is longer and more slender in ♀.

Length ♀, 21–24 mm.; abdomen 16–18 mm.; petiole 10–11½ mm.; terebra 20–22 mm.; ♂, 21 mm.

Habitat: Aden; Ruaha River, late German East Africa.

This species appears to differ from *S. gigas* Schlett. in the formation of the prothorax and in the strikingly incrassate hind femora.

In some respects it resembles *S. pachylomerus* Schlett., from which it may be distinguished by the coarsely punctate temples, formation of the prothorax, and by the shorter petiole and terebra.

It resembles *S. antinorii* in size, length of terebra, and incrassate hind femora—this last is not uncommon among the African species. It differs in the longitudinal occipital sulcus, structure and sculpture of prothorax, formation of mesothorax and sculpture of mesopleuræ.

*S. tibiator* ♂ is distinguished from all others yet known by the hind tarsi being three-jointed, and is the only known exception to the rule, that the males of this family have those tarsi five-jointed.

*S. serrator* ♀ alone has the hind tarsi five-jointed, otherwise they are invariably three-jointed.

##### 5. NIGRICAUDA Sichel.

*Megischus nigricauda* Sichel (2), p. 479, ♀. *Stephanus n.* Schlett., p. 106, ♀.

♀. Frons coriaceo-granulate, vertex arcuate rugose; occiput with basal third trans-striate, remainder smooth polished. Pronotum smooth and shining, neck subquadrate; mesonotum almost impunctate, smooth and shining; with an anterior longitudinal impression, separated from the smooth polished scutellum by a row of punctures; median segment scrobiculate reticulate. Petiole finely trans-striate, remainder of abdomen smooth polished. Terebra as long as body, sheaths black. Legs, especially the hind ones, smooth and shining; hind femora bidentate.

Black; head red, vertex black, cheeks pale marked; mandibles basally and two or three basal antennal joints red or rufescent; anterior tarsi rufous, middle tarsi white-banded, base of hind

metatarsus and whole of following joints white, claws black. Wings flavescent, costa beyond stigma black; nervures fuscous.

Length of body and terebra 15–16½ mm. Wings 8–8½ mm.

Habitat: Manila (Luzon). Prof. Semper. 2 ♀ ♀.

Sichel remarks on the variability of the serrations between the large teeth. In one specimen one of these, near the apex of femora, amounts almost to a third tooth, while on the other specimen this is present on one femur only.

The coriaceo-granulate frons, the very smooth pro- and mesonotum, and the apparent absence of all sculpture on the legs suffice to distinguish this species.

#### 6. PACHYLOMERUS Schlett.

*Stephanus pachylomerus* Schlett., p. 98, ♀; Morley (1), p. 111.

♀. Frons coarsely arcuate rugose; vertex very convex and arcuate to transverse rugose; occiput transrugose. Posterior margin of head simple. Temples centrally prominent, very shining; cheeks shorter than scape. Second flagellar joint more than twice as long as first, third only as long as second. Neck very short, with a deep oblique impression, and superficially punctate-rugose; semiannular polished, with very diffuse fine punctures. Mesonotum with medium-sized and partly confluent punctures. Scutellum smooth, margins of lobes obliquely striate. Mesopleuræ with the upper impressed part oblique rugose in front, smooth behind, the lower convex part diffusely punctate. Metapleuræ coarsely and irregularly rugose, separated from the cribrate-punctate median segment by a deep, slightly rugose sulcus. Petiole finely transrugose, distinctly shorter than the rest of abdomen; second segment shining smooth, basally feebly rugose, the remainder rather dull. Terebra longer than body, its sheaths entirely black. Hind legs with coxæ strongly shining, diffusely punctate; femora very incrassate, smooth, diffusely punctate, bidentate; tibiæ slightly longer than femora, compressed nearly to middle.

Black; head, base of mandibles, scape, third segment entirely and legs partly red; apical abdominal segments more or less rufescent. Wings subhyaline, discal and external submedian cells infusate.

Length 28 mm.; terebra 35 mm.

Habitat: West Africa (Gaboön); type in Nat. Hist. Museum, Hamburg. Gold Coast; in coll. British Museum.

This species resembles *S. coronator* and *ducalis* in shape and colour, but may be easily distinguished by the entirely black sheaths of the terebra, prominent temples, weaker puncturation of mesothorax and more incrassate hind femora. From *S. subcifrons*, which it also resembles, it may be known by the absence of the sulcus on vertex and by the simple posterior margin of head. It differs from *S. xanthocephalus* Cam. in the short pronotum, sculpture of prothorax and hind coxæ, and in coloration.

## 7. XANTHOCEPHALUS Cam.

*Stephanus xanthocephalus* Cameron (10), p. 358, ♀.

♀. Frons strongly arcuate striate; vertex irregularly arcuate rugose, occiput finely and closely trans-striate; posterior margin of head simple. Pronotum densely and rather strongly trans-striate; mesonotum shining, irregularly striate and punctate, basal half centrally smooth. Scutellum smooth, apically sparsely punctate. Pleuræ smooth, white pubescent. Median segment with large, diffuse punctures, apically irregularly trans-striate. Petiole finely and closely striate, apically more strongly, longer than rest of abdomen. Terebra half as long again as body, sheaths entirely black. Hind legs with coxæ densely striate, femora with two large teeth, one medium and two very small.

Black; head pale yellow, with broad black band from occiput to posterior tubercles; scape testaceous; antennæ black; third segment partly, ventral surface and apical segment entirely rufous; apices of femora, anterior tibiæ and tarsi, apex of hind tibiæ, and hind metatarsus rufo-testaceous. Wings hyaline, posterior discoidal cell infumate, stigma and nervures black.

Length 28 mm.; terebra 43 mm.

Habitat: Dima, West Africa. A. Koller. Type in Congo Museum, Tervouren.

The pale yellow, black-banded head is very distinctive.

## 8. SULCIFRONS Schlett.

*Stephanus sulcifrons* Schlett., p. 110, ♀. ? *Megischus insidiator* Smith (3), p. 7 ♂.

♀. Frons coarsely and obliquely to irregularly rugose, vertex transrugose, the rugosity gradually passing into puncturation on occiput, and all sculpture disappearing at back of head; a very distinct longitudinal sulcus across vertex and part of occiput; posterior margin of head strongly bordered; cheeks rather shorter than scape. Second flagellar joint twice as long as first, third shorter than first and second together. Neck coarsely and obliquely rugose; semiannular rather closely and partly confluent punctate, its posterior margin polished smooth. Mesonotum diffusely and coarsely punctate. Scutellum smooth, with a few conspicuous marginal punctures. Mesopleuræ feebly rugose and shining in the upper impressed part, punctate below; metapleuræ very coarsely and densely punctate, separated from the coarsely cribrate-punctate median segment by a deep and smooth sulcus. Petiole transrugose, apically smoother, shorter than rest of abdomen, which is basally shining, otherwise dull. Terebra much longer than body, sheaths entirely black. Hind legs with coxæ coarsely transrugose; femora entirely smooth, bidentate, the tibiæ longer than femora, compressed to beyond middle.

Black; head, two basal antennal joints, anterior legs and hind tarsi red or ferruginous. Wings slightly infusate, centrally darker.

Length 23 mm.; terebra 30 mm.

Habitat: Mindanao, Philippines. Type in Museum at Hamburg.

♂ (?). *M. insidiator*, Smith. "Male. Length 9 lines. The head and base of the antennæ ferruginous; the former transversely striated, with the posterior margin of the vertex smooth and shining, or with a few punctures. Thorax strongly, but not closely punctured; wings fusco-hyaline, the anterior and intermediate tibiæ rufo-testaceous, with the femora obscurely so; the posterior femora with two stout teeth beneath and six minute ones between them; the posterior tibiæ at their apex, and the tarsi pale rufo-testaceous. The abdomen elongate, lanceolate at the apex, and entirely smooth and shining. *Hab. Mysol.*"

This species may be best known from the very similar *S. coronator* F. by the sulcus on vertex and entirely black terebral sheaths; the latter character and the smaller size will distinguish it from *S. ducalis* Westw. Smith's description of his *insidiator* is defective, but it may be the male of *sulcifrons*, which it appears to resemble.

#### 9. BRUNNEUS Cress.

*Megischus brunneus* Cresson (1), p. 84, ♀ ♂.

♀. Head coarsely rugose, vertex deeply trans-striate. Thorax coarsely and confluent punctate; apex of median segment trans-rugose. Petiole trans-striate, remaining segments shining smooth. Terebra longer than body, spicula brown, sheaths blue-black. Hind femora bidentate, the anterior tooth largest; hind tibiæ compressed in basal third; hind tibiæ 3-jointed, metatarsus much dilated. All tarsi yellow pubescent beneath.

Dark chestnut-brown, antennæ blackish, scape brown, legs brown, knees yellowish, posterior femora and tibiæ externally nigrescent. Wings subhyaline, tinged with fuscous; stigma and nervures black, former with basal pale spot.

Length 1-11 lines (14-23 mm.); terebra 9-13½ lines (18-27 mm.); fore wings 9½-14½ lines (19-29 mm.)

♂. Similar to ♀, but more slender; the two teeth on hind femora equal in size, hind tibiæ less dilated, all tarsi five-jointed, hind metatarsus not dilated.

Length 9 lines (18½ mm.); alar expanse 9½ lines (19 mm.)

Habitat: Cuba.

"Collection Ent. Soc. Philad. Two ♀ ♀, two ♂ ♂ specimens. Both ♂ and ♀ of this species were taken by Dr. Gundlach in considerable numbers, coming out of the same hole in the trunk of a diseased tree, called *Jalia* in Spanish."

#### 10. UNICOLOR Schlött.

*Stephanus unicolor* Schlött., p. 104, ♀.

♀. Frons rather coarsely and irregularly to arcuately rugose; occiput transrugose, more coarsely near the ocelli; posterior margin of head with raised border; cheeks as long as scape.



Second flagellar joint one and a half times as long as first, third fully twice as long as first, but shorter than first and second together. Neck very short, laterally coarsely rugose, bifoveate above; semiannular smooth and shining, with a few anterior and lateral superficial punctures. Mesonotum diffusely punctate, with a distinct row of central punctures. Scutellum polished smooth, with a few lateral punctures. Mesopleuræ smooth above, feebly rugose and diffusely punctate beneath; metapleuræ coarsely reticulate to irregularly rugose, separated by a smooth shining sulcus from the median segment, which is reticulate to cribrate punctate. Petiole moderately coarsely transrugose, little shorter than the rest of abdomen, the central segments more or less dull, the basal and apical segments shining smooth. Terebra as long as body, sheaths entirely black. Hind legs with coxæ coarsely transrugose; femora stout and polished, bidentate; tibiæ compressed to beyond middle.

Black; the head shows a tendency to become red on the frons, pale yellow on cheeks and temples; scape ferruginous, anterior legs brown to rufescent. Wings slightly infusate.

Length 14 mm.

Habitat: Mindanao, Philippines. Type in Nat. Hist. Museum, Hamburg.

This species is somewhat similar to *S. sulcifrons* Schlett., but only half as large and wanting the distinctive vertical sulcus. It also resembles *F. indicus* West., *D. leucodontus* Schlett., and *D. pallescens* Schlett., from all of which it may be known by the neuration.

#### 11. HORNIANUS Enderl.

*Stephanus hornianus* Enderl. (5), p. 12, ♀ ♂.

♀ ♂. Frons coarsely transrugose; vertex with four transcarinae; occiput irregularly rugose. Second flagellar joint shorter than third. Neck trans-striate; semiannular smooth polished, with a row of punctures before posterior margin. Propleuræ trans-striate, mesopleuræ smooth, lower half punctate, apex subrugose; metapleuræ widely reticulate, separated from the median segment by a very deep, smooth, and shining sulcus. Median segment widely reticulate, basally diffusely punctate, apically densely transrugose. Petiole finely trans-striate, as long as, or slightly shorter than remainder of abdomen. Terebra in ♀ rather longer than body. Hind legs with coxæ shining smooth, diffusely punctate, transrugose in front and behind; femora diffusely punctate, bidentate.

Black; a yellow spot on outer orbits; petiole and legs except coxæ and hind femora ferruginous; last tarsal joint black. Wings subhyaline, with red and green transverse iridescence on outer margin; stigma and nervures black.

Length? Habitat: Ceylon.



Enderlein appears not to have given the size of this species, but as he compares it with *S. ceylonicus* Cam. and *S. hæmatipoda* Montrz., it is probably about 28–30 mm. The former of the above species is said to resemble the present one in colour, with the same spot on the outer orbits, but the sculpture of the meso- and meta-pleuræ differs, the petiole is black, and the wings have a steely iridescence.

## 12. ANDINUS Schlett.

*Stephanus andinus* Schlett., p. 138, ♀.

♀. Frons somewhat coarsely and irregularly rugose; occiput transrugose, coarsely in front, more regularly towards the eyes. Temples finely but distinctly obliquely rugose, with a smooth space behind eyes. Posterior margin of head simple. Second flagellar joint twice as long as first, third a little shorter than first and second together. Neck rather coarsely transrugose; semiannular finely but distinctly obliquely rugose. Mesonotum coarsely and confluent punctate, the usual median row of punctures wanting and the two lateral impressions represented by indistinct rows of punctures. Scutellum coarsely and diffusely punctate. Mesopleuræ above finely alutaceous and dull, beneath slightly shining and diffusely punctate; metapleuræ dull, finely and diffusely punctate, separated from median segment by a deep and dull sulcus. Median segment diffusely but deeply punctate, apically transrugose and with distinct lateral sulci. Petiole trans-striolate, basally more irregularly rugose, shorter than rest of abdomen, which is discally dull, laterally shining. Terebra as long as body, sheaths white-banded before apex. Hind legs with coxæ trans-striolate; femora shining smooth, bidentate; tibiæ constricted not quite to middle.

Black; cheeks pale marked; the anterior legs, especially the tarsi, tend to become brownish. Wings hyaline.

Length 19–20 mm.

Habitat: Colombia. Type in Royal Nat. Hist. Museum, Berlin.

This species differs from *S. acutus* Lep. & Serv. in the simple posterior margin of head, coarser puncturation of mesonotum, and shorter petiole. From *S. niger* Smith it may be known by the finer sculpture of the frons, obliquely rugose temples, and rugose semiannular.

## 13. SICKMANNI Schlett.

*Stephanus sickmanni* Schlett., p. 152, ♀.

♀. Frons coarsely and irregularly rugose; occiput anteriorly arcuately, posteriorly transversely, and laterally irregularly rugose. Temples with a few apical punctures. Posterior margin of head simple. Cheeks slightly longer than scape. Basal flagellar

joints normal. Neck coarsely transrugose, semiannular distinctly transrugose and finely punctate, with smooth posterior margin. Mesonotum coarsely and irregularly rugose-punctate. Scutellum centrally smooth, laterally with diffuse to dense and partly confluent punctures, lateral lobes smooth in front, densely and confluent punctate behind. Mesopleuræ above distinctly alutaceous, shining smooth, with diffuse punctures below; metapleuræ diffusely punctate, more densely in front, separated from median segment by a very shallow and alutaceous sulcus. Median segment rather coarsely and diffusely punctate, longitudinally rugose round insertion of petiole, marginal furrows indistinct. Petiole centrally smooth, basally and apically somewhat rugose, shorter than remainder of abdomen, which is apically dull. Terebra about as long as body, sheaths white-banded before apex. Hind legs with coxæ coarsely transrugose above, laterally more irregularly; femora subglabrous, bidentate; tibiæ compressed not quite to middle.

Black; cheeks pale marked; antennæ, mandibles basally and the legs, especially about the joints, tend to become rufous. Wings almost hyaline.

Length 24-25 mm.

Habitat: Georgia, U.S.A. Type in Royal Nat. Hist. Museum, Berlin. Named after Prof. Franz Sickmann, of Iburg, Hanover.

This species resembles small individuals of *S. furcatus* Lep. & Serv., from which it differs in the shorter petiole and terebra, and sculpture of prothorax and mesonotum. For differences between this species and *S. bicolor* Westw., see the latter species. It bears also a great resemblance to *H. marginalis* Schlett., but is easily distinguished by the neurulation and by the reflexed posterior margin of head in latter.

#### 14. CRASSICAUDA Morley.

*Stephanus crassicauda* Morley (1), p. 106, ♀.

♀. Head coarsely and irregularly rugose, a central longitudinal trans-striate sulcus on occiput; posterior margin of head simple; temples finely punctate, prominent and glabrous above. Second and third flagellar joints of equal length and a little longer than first. Neck short, with three strong trans-carinæ; semiannular finely trans-striate, its posterior margin narrowly smooth; mesonotum coarsely punctate; scutellum smooth, with diffuse and rather fine puncturation. Meso- and metapleuræ alutaceous and dull, with a few punctures, latter separated from the median segment by a sulcus. Median segment scabriculous and centrally trans-striate. Petiole trans-striate, as long as rest of abdomen; apical segments discally emarginate. Terebra slightly longer than body, sheaths unusually stout and abruptly pointed, ferruginous, with a white band before the equally broad black apex. Hind legs with coxæ elongately pilose and sparsely trans-

carinate; femora smooth and pilose, with two very long and slender teeth; tibiæ constricted in basal third and again beyond middle.

Black; a white spot on cheeks; base of flagellum ferruginous; anterior legs, hind trochanters, constricted part of tibiæ, their apex, and the hind tarsi fulvous. Wings slightly infumate, external submedian cell darker, with a pale space beyond it.

Length 26 mm.; abdomen 16 mm.; petiole 8 mm.; terebra 27 mm.

The type, in the British Museum, bears a label "Australia, 1868" only.

The cotype, in same collection, is much smaller: body  $20\frac{1}{2}$  mm.; abdomen 13 mm.; petiole 6 mm.; terebra 19 mm. It was taken by F. P. Dodd, 5. iii. 08, at Townsville, Queensland.

#### 15. TARSATUS Sichel.

*Megischus tarsatus* Sichel (2), p. 476, pl. 10, figs. 4 et 5, ♀.  
*Stephanus tarsatus* Schlett., p. 107, ♀ ♂.

♀. Face below antennæ obliquely striate, the striæ descending from the sides to the central line; frons transrugose; vertex coarsely transrugose; occiput with a small central part transrugose, laterally irregularly reticulate. Neck elongate, transrugose; mesonotum apically smooth, centrally diffusely punctate with a few transrugosities; scutellum smooth, with deep and coarse but diffuse punctures; median segment scrobiculate reticulate. Abdomen slightly pubescent; petiole trans-striate. Terebra as long as body, white-banded before apex. Hind coxæ trans-striate; hind femora bidentate.

Black; head except apex of mandibles, scape, sometimes also basal flagellar joint, apex of pronotum, anterior femora, tibiæ mostly, and the tarsi red; antennæ fusco-piceous. Wings infumate, nervures fuscous or rufo-fuscous.

Length 38 mm. Expanse of fore wings 18 mm.

♂. Similar to ♀; head more strongly transrugose, occiput centrally more broadly trans-striate, metathorax more rugose, petiole and coxæ more finely sculptured, serrations on hind femora finer; abdomen fusco-piceous.

Length 24 mm. Expanse of fore wings 11 mm.

Habitat: Manila, Philippines; Bachian, Molucca Islands.

Schletterer (*l. c.*) tentatively synonymizes this with *M. tarsalis* Smith, from Bachian; remarking that it corresponds in the infumation of the wings, length and colour of terebra, colour of body, sculpture of petiole, and, to some extent also, in sculpture of head and thorax. It appears, however, to differ in having the head coarsely sculptured, black, not red as in *tarsatus*, the thorax coarsely punctate, and is only 9 lines (18 mm.) long. I consider it a distinct species, but the description is insufficient for certain determination.

16. *TEXANUS* Cress.

*Megischus texanus* Cress. (2), p. 190, ♀.

♀. Frons coarsely reticulate; vertex with two trans-carinae; occiput finely transrugose. Pronotum smooth; mesonotum coarsely rugose; metanotum (median segment) centrally and apically rugose. Petiole as long as rest of abdomen. Terebra as long as body, basal half of sheaths ferruginous, apical half black, white-banded before apex. Legs shining; hind femora bidentate; hind tibiae constricted above middle. Wings "too much damaged to be described."

Opaque, dull ferruginous; head yellowish, mandibles apically black; antennae apically darker; hind tibiae with constricted part yellow: frontal tubercles apically and abdominal segments from second apically fuscous.

Length 10 mm.

Habitat: Comal Co., Texas. 1 ♀.

In the absence of details as to the wings, I place this species in the subgenus *Stephanus*. It appears to be characterized by the sculpture of the head and by the colour, especially of the terebral sheaths.

17. *EUROPÆUS* Sichel.

*Bothriocerus europæus* Sichel (1), 1860, p. 759, ♀. *Megischus eur.* Sichel (2), p. 484, ♀. *Stephanus eur.* André, p. 486; Schlett., p. 95, ♀.

♀. Head granulate, frons near tubercles irregularly rugulose, occiput above regularly transrugose. Pronotum irregularly trans-striate, its extreme posterior margin smooth; mesonotum coriaceo-granulate, obscurely trans-striate, with central longitudinal row of punctures; median segment coriaceo-granulate and apically obscurely trans-striate. Petiole trans-striate, basally smooth, remainder of abdomen smooth and shining. Terebra longer than body, its sheaths apically white-banded. Legs smooth.

Black; mandibles and antennae basally rufo-testaceous; tegulae, petiole, base of second segment, trochanters, anterior tibiae, hind tibiae basally, and all tarsi red or rufescent. Wings subhyaline, stigma black, nervures fuscous.

Length 13 mm.; terebra 17 mm.

The unique specimen was taken in Sicily in Sept. 1859.

In the absence of details as to the relative lengths of the antennal joints and of the hind legs, it is impossible to place this species with certainty. It appears to be very near *anomaliipes* Fst., from which it differs chiefly in the basally smooth petiole. The granulate sculpture is probably the same as that otherwise described as coarsely punctate. A similar case occurs where the same sculpture is described by one author as "coarsely striate" and by another as "carinate."



18. *TORTUS* Morley.*Stephanus tortus* Morley (1), p. 84, ♀.

♀. Frons reticulately, but not transversely rugose; the three anterior tubercles prominent, acute; occiput laterally coarsely reticulate, centrally transaciculate; posterior margin of head simple. Second flagellar joint rather longer than first, third only as long as second. Neck transrugose, semiannular glabrous. Mesonotum smooth, central row of punctures distinct, lateral rows subobsolete. Mesopleuræ smooth above, rugulose beneath; metapleuræ rugulose, separated from the median segment by a strong, glabrous sulcus. Median segment deeply and rather diffusely punctate, apically transaciculate. Petiole shorter than rest of abdomen, finely trans-striate throughout, all remaining segments smooth shining. Terebra about one-third longer than body, sheaths white-banded before apex. Hind legs with coxæ discally glabrous and finely granulate, below and inside obsoletely trans-striate; femora bidentate, shining smooth, sparsely punctate; tibiæ compressed in basal third, centrally excised and apically inflated.

Black; mandibles and a spot near their base red; petiole dark red, rest of abdomen piceous; anterior legs, except basally, red; hind tibiæ piceous, centrally red. Wings slightly infumate.

Length 26 mm.; abdomen 19 mm.; petiole 9 mm.; terebra 34 mm.

Habitat: Nedunkernie, N.P. India. Taken by O. S. Wickwar.

Type in coll. Claude Morley, Monk Soham, Suffolk.

The proportions of the flagellar joints, granulate hind coxæ, and structure of hind tibiæ distinguish this species from all others with white-banded terebral sheaths.

19. *ANOMALIPES* Fst.

*Stephanus anomalipes* Först., p. 228, ♀; Schlett., p. 93; André, p. 487, ♀.

♀. Frons rather coarsely and irregularly rugose; occiput diffusely and arcuately rugose behind the tubercles, posteriorly transversely, laterally irregularly rugose. Temples with a few shallow and confluent punctures in front; posterior margin of head simple. Second flagellar joint twice as long as first; third longer than second, but shorter than first and second together. Neck rather coarsely and transversely, semiannular more finely and less regularly rugose. Mesonotum rather coarsely, posteriorly more densely transrugose punctate, with a distinct central longitudinal line of punctures and two lateral impressions. Scutellum centrally shining smooth, laterally finely and densely punctate. Mesopleuræ rather coarsely coriaceous throughout; metapleuræ coarsely and irregularly rugose, separated by a distinct and slightly alutaceous sulcus from the median segment, which is coarsely and densely rugose-punctate. Petiole rather slender, finely coriaceous, basally indistinctly transrugose,



shorter than the remaining segments together, also shorter than the hind coxæ, trochanters and femora together; rest of abdomen basally rugose, thence dull to apex. Terebra longer than body, its sheaths white-banded before apex. Hind legs with coxæ plainly trans-striate above, laterally coriaceous and shining; femora internally shining, externally and above almost shining, slightly rugose behind, bidentate; tibiæ longer than femora, compressed in basal third.

Black; cheeks pale marked, mandibles and antennæ basally ferruginous, temples tending to brownish; abdomen brown, petiole rufescent; legs more or less rufescent. Wings slightly infumate throughout.

Length 17 mm.; terebra 21 mm.

Habitat: Hungary. Förster's type is in the State Museum at Budapest.

Distinguished from *serrator* Fab. by the three-jointed hind tarsi, white-banded terebral sheaths, etc. From *S. sickmanni* Schlett. it may be known by the rugose, not punctate metapleuræ, coriaceous petiole, and longer terebra.

## 20. BICOLOR Westw.

*Stephanus bicolor* Westw. (2), p. 535; (3), p. 276; Schlett., p. 154, ♀.

♀. Frons arcuately to irregularly rugose; occiput anteriorly arcuately, posteriorly rather coarsely transversely, laterally more irregularly rugose. Temples very diffusely punctate. Posterior margin of head simple. Cheeks a little longer than scape. Basal flagellar joints normal. Neck rather coarsely transrugose; semiannular finely transrugose and sparsely punctate. Mesonotum rather coarsely punctato-rugose. Scutellum smooth, with a few punctures on outer margin only. Mesopleuræ above alutaceo-rugose, below somewhat densely punctate; metapleuræ irregularly rugose, separated from the median segment by a nearly smooth sulcus. Median segment rather densely punctate centrally, laterally more diffusely, oblique to transverse rugose round insertion of petiole, crenulate marginal sulci distinct. Petiole basally irregularly, otherwise transversely striate, shorter than remainder of abdomen, which is entirely dull. Terebra evidently longer than body, sheaths white-banded before apex. Hind legs with the coxæ laterally coarsely and irregularly, above indistinctly, apically decidedly transrugose; femora slightly shining, bidentate; tibiæ compressed to middle.

Badius; head and thorax ferruginous, remainder of body red-brown; petiole more or less nigrescent. Wings slightly infumate.

Length 15–22 mm. Habitat: Kentucky, Georgia, U.S.A.

This species may be known from *S. sickmanni* Schlett., which it much resembles, by the longer terebra, sculpture of meso- and meta-pleuræ and of petiole, which is rugose throughout, not centrally smooth. The colour is also distinctive, being a decided red-brown or chestnut, *S. sickmanni* being deep black.

21. *NIGRICANS* (Sichel), Schlett.

*Megischus tarsatus* var. *nigricans* Sichel (2), v, p. 476, ♀.  
*Stephanus nigricans* Schlett., p. 109, ♀.

♀. Face below antennæ irregularly rugose reticulate, frons transrugose; occiput centrally broadly transrugulose, laterally coarsely and deeply reticulate. Neck elongate, transrugose; mesonotum diffusely punctate; scutellum centrally smooth, laterally diffusely punctate; median segment coarsely reticulate. Petiole trans-striate; terebra longer than body, broadly white-banded before apex. Hind coxæ trans-striate; hind femora bidentate.

Black; tegulæ apically rufescent; anterior legs red, front femora externally black. Wings infumate, nervures fuscous.

Length 33 mm.; fore wings 12 mm.; terebra 35 mm.

Habitat: Ceylon. One ♀ in coll. Sichel.

Sichel considers this a variety of *S. tarsatus* Sichel, which it strongly resembles, but the different sculpture of face and occiput, black head, and longer terebra entitle it to specific rank.

22. *NIGER* Smith.

*Megischus niger* Smith (4), i. p. 44; Cam. (1), p. 420, pl. xviii. fig. 19, ♀. *Stephanus niger* Schlett., p. 135, ♀.

♀. Frons coarsely and irregularly rugose; occiput anteriorly arcuate-rugose, posteriorly transversely, laterally irregularly rugose; cheeks scarcely as long as scape. Posterior margin of head strongly bordered. Second flagellar joint two-and-a-half times as long as first, third as long as first and second together. Neck with a distinct transverse impression, behind which it is finely and sparsely rugose; semiannular polished, with very fine and diffuse punctures. Mesonotum finely trans-striate and diffusely punctate, the usual central row of punctures and the two lateral impressions obsolete. Scutellum smooth, with a few marginal punctures. Mesopleuræ smooth, with diffuse coarser and finer punctures; metapleuræ finely and irregularly rugose, separated by a deep and smooth sulcus from the median segment, which is diffusely and irregularly punctate, with distinct marginal furrows. Petiole very distinctly trans-striate, much shorter than remainder of abdomen, but nearly as long as the hind coxæ, trochanters, and femora together. Terebra scarcely longer than body, its sheaths white-banded before apex. Hind coxæ trans-striate between stronger rugosities; hind femora dull, bidentate; tibiæ compressed not quite to middle.

Black; cheeks pale marked and the anterior legs with a tendency to brown. Wings hyaline.

Length 23–25 mm.

Habitat: Panama, Guatemala. Type in British Museum.

This species is distinguished from the similar *S. marginalis* Schlett. by the bordered but not reflexed posterior margin of

head, shorter petiole, and by the sculpture of prothorax and median segment.

*S. sickmanni* Schlett. has the posterior margin of head simple, neck of prothorax short, semiannular rugose-punctate, and mesopleuræ punctate.

### 23. FROGGATTII Cam.

*Megischus froggattii* Cameron (9), p. 357, ♀ ♂. *Stephanus froggattii* Cam. (11), p. 98; Elliott (2), p. 28, ♀ ♂. *Stephanus rubripes* Morley (1), p. 107, ♀ ♂.

♀ ♂. Frons strongly transrugose; vertex arcuately and occiput transversely rugose; cheeks shorter than scape; posterior margin of head bordered. Second and third flagellar joints of equal length and rather longer than first. Neck short, centrally longitudinally impressed, with one strong basal carina; semiannular widely aciculate, extreme base smooth. Mesonotum coarsely punctate, with central smooth space; mesosternum flat and polished. Scutellum smooth, basally bounded by a crenulate furrow. Propleuræ diffusely punctate; mesopleuræ smooth above, with three or four irregular rows of punctures below; metapleuræ closely rugulose throughout, separated by a smooth sulcus and a carina from the median segment, which is rather densely but superficially punctate. Petiole transaciculate, a little shorter than the remaining segments together; base of second segment feebly rugose, rest smooth and shining. Terebra as long as, or very slightly longer than body, sheaths black, broadly white-banded before apex. Hind legs with coxæ slender and strongly trans-striate; femora smooth and shining, bidentate; tibiæ longer than femora, constricted in basal third; tarsi five-jointed in ♂, three-jointed in ♀; all tibiæ and the hind femora elongately pilose.

Black; mouth-parts and genal orbits testaceous; anterior legs except coxæ and trochanters bright red; hind femora and tarsi, except apically, and apical two-thirds of hind tibiæ red. Wings brown, centrally darker, stigma and nervures black.

Length, ♀, 33 mm.; abdomen 22 mm.; petiole 10 mm.; terebra 35 mm.; ♂, 16 mm.; abdomen 11 mm.; petiole  $4\frac{1}{2}$  mm. Another ♂, 12, 8,  $3\frac{1}{2}$  mm. Taken by W. W. Froggatt, Solomon Islands, July-Aug. 1909.

♀ ♂, length 22 mm.; abdomen 13 mm.; petiole 6 mm.; terebra in ♀,  $21\frac{1}{2}$  mm. Taken by C. M. Woodford, Solomon Islands, 1887.

There are also in the British Museum 5 ♀ ♀, 2 ♂ ♂, their dimensions lying between those given above.

Cameron states that the abdominal petiole is a little longer than the rest of abdomen, but actual measurement shows it to be shorter. He also gives the colour of the wings as fusco-violaceous; it is now brown; possibly faded.

This species much resembles *S. rufo-femoratus* Szépl., also from the same locality, but differs in the relative length of the basal joints of the antennæ, sculpture and length of petiole, and the strongly trans-striate hind coxæ.

Cameron considers it to be near his *Megischus violaceipennis* from New Britain, in which the sculpture of the body tends to be reticulate.

Mr. C. T. Brues found in the Museum of Harvard College 4 ♀ ♀, 2 ♂ ♂, from Auki, Tulagi, Fulakora, and Malaili. The larger females, 26–31 mm., have the femoral teeth more strongly developed than in the smaller individuals of 21–23 mm. The males measure from 20–21 mm.

#### 24. CEYLONICUS Cam.

*Stephanus ceylonicus* Cam. (4), p. 102; Morley (1), p. 34, ♀.

♀. Frons irregularly transrugose, arcuately above; vertex and occiput arcuate rugose; posterior margin of head finely bordered. Second flagellar joint twice as long as first, third little longer than second. Neck closely trans-striate, with central apical row of punctures, semiannular transcarinate, laterally diffusely punctate, a narrow posterior margin smooth. Mesonotum diffusely punctate; scutellum only laterally punctate. Propleuræ closely obliquely striate; mesopleuræ almost impunctate; metapleuræ smooth above, coarsely and almost reticulately transrugose beneath. Median segment diffusely punctate, apically transreticulate. Petiole closely trans-striate, as long as rest of abdomen, which is smooth. Terebra slightly longer than body, sheaths white-banded before apex. Hind coxæ transrugose, hind femora bidentate.

Black; a pale spot below eyes; anterior legs and base of hind tibiæ rufo-testaceous. Wings hyaline with steely iridescence; stigma and nervures black.

Length 28 mm.

Habitat: Trincomali, Ceylon (Yerbury). Kandy and Galle, Ceylon (Morley.)

#### 25. BORNEENSIS Sauss.

*Megischus borneensis* Sauss., p. 202, ♀ ♂.

“♀ ♂. *M. ruficeps* simillimus, ejusdem pictura; capite tamen toto rufo; tantum mandibulæ apice nigris. Antennæ nigrae, primo articulo rufo. Caput sicut in specie, laudata inculptum sed superne totum et occipite transverse arcuato-strigatum. Facies rugoso-punctata, nonnunquam tamen utrinque strigis nonnullis, valde obliquæ conferens, vel toto transverse obsoleta arcuata-strigata. Mesonotum politum, cribrosum, antica utrinque punctis confluentibus crasse strigatus; scutello polito. Coxæ postice transverse elevato-rugatæ ac striatæ. Femora postica, denti usque 3 armata (1 ante medium, 2 prope



apicem). Alæ fusco nebulosæ, in medio vitta transversa vel maculis fusca.

"Variet. *a*. Pedibus fusco-rufescentibus.

*b*. In individuis minoribus et in maribus sculptura incomplete explicata.

"♀. Long. 20-31; thoracis 4·8-7·5; petioli 6-10; oviposit. 32·5-40 mm.

"♂. Long. 25; thoracis 4·6; petioli 6·5; alæ 12 mm."

Habitat: Borneo.

Very similar to *furcatus* Lep. & Serv. and to *ruficeps* Sauss., but distinguished from both by the tridentate hind femora and the central dark mark or band in fore wing; from the latter also by the sculpture of the frons, and the longer terebra.

## 26. *FURCATUS* Lep. & Serv.

*Stephanus furcatus* Lep. & Serv., p. 1835, ♀; Schlett., p. 130, ♀ ♂. *Stephanus brasiliensis* Westw. (1), p. 413, pl. 66, fig. 3; Westw. (3), p. 227, ♂. *Megischus annulator* Brull., p. 539, pl. 40, fig. 5; Sichel (2), p. 482, ♀; Cam. (1), p. 419, pl. 18, fig. 7, ♂. *Stephanus annulator* Westw. (3), p. 228, ♀. *Bothriocerus americanus* Sichel (1), p. 761, ♀. *Megischus americanus* Sichel (2), p. 480, ♀. *Megischus brasiliensis* Sichel (2), p. 483, ♂.

♀ ♂. Frons very coarsely irregularly to arcuately rugose; the three anterior tubercles very large; occiput coarsely rugose, arcuately in front, transversely behind, laterally irregularly. Temples apically feebly rugose; cheeks as long as scape. Posterior margin of head strongly bordered. Second flagellar joint fully twice as long as first, third longer than second but shorter than first and second together. Neck coarsely transrugulose, semiannular smooth, slightly transrugose in front and with a few lateral punctures. Mesonotum with a central row of very coarse punctures, a smooth, diffusely punctured space on each side bounded by divergent impressions, beyond which it is laterally transrugose, with a more or less extensive smooth space. Scutellum polished and diffusely punctate. Mesopleuræ finely coriaceous above, obliquely rugose in front, smooth and diffusely punctate beneath; metapleuræ with a few coarse rugosities in which are some large punctures, separated from the median segment by a shallow but distinct and almost smooth sulcus. Median segment punctate, more densely and partly confluent centrally and laterally, apically transrugose. Petiole trans-striate, shorter than rest of abdomen, also shorter than the hind coxæ, trochanters and femora together; second segment shining smooth, basally rugose, remaining segments rather dull. Terebra longer than body, white-banded before apex. Hind legs with coxæ finely transrugose between coarse, scale-like rugosities; femora shining smooth, bidentate; tibiæ compressed not quite to middle; tarsi five-jointed in ♂, three-jointed in ♀.



Black to dark brown, cheeks sometimes pale marked. Wings infumate.

Length 25–39 mm.; terebra in ♀, 38–52 mm.

Habitat: Brazil; Guatemala.

The sculpture of the median segment is variable. In some specimens in the British Museum the punctures are more diffuse, only apically and laterally confluent, forming transverse rugosities; in others the punctures are more confluent, the greater part of the segment being coarsely transrugose. The punctures appear to be more distinct in the ♂♂ than in the ♀♀.

*S. annulator* Brull., ♀♂; the types are in the British Museum, and certainly belong to the present species. ♀: length 25 mm.; terebra 27 mm.; abdomen, anterior legs, and hind tibiæ rufescent. ♂: length 23 mm.; the front legs and hind tibiæ red.

*S. brasiliensis* Westw., ♀. Type in British Museum. This is a very small specimen, only 17 mm. long, terebra 20 mm., with abdomen and all tarsi rufescent. I cannot find any specific difference from *furcatus* Lep. & Serv.

This species is said to be the least rare of the family. It can be distinguished from *S. sickmanni* Schlett. by the raised posterior margin of the head, sculpture of thorax, and longer terebra. It also superficially resembles *Hemistephanus marginalis* Schlett., but may be at once distinguished by the neururation of the wings.

## 27. RUFICEPS SAUSS.

*Megischus ruficeps* Sauss., p. 201, ♀. *Stephanus saussurei* Schulz (2), p. 322, ♀.

“Ba Chieu, prov. Saigon, 1886; Cambodia, 1886.

“♀. Validus, cinereo-hirtus, *M. furcati* Brull. statura et illi simillime. Caput rufus, ore nigrò, palpis fuscis. Antennæ nigrae, basi superne rufæ, primo articulo rufo. Caput antèrius rugato-punctatum, haud arcuato strigatum, supra crassissime areolato-punctatum, in vertice rugis transversis elevatis 1–4 instructum; occipitis vitta longitudinali transversa striata. Frontis depressis subrhomboidalis, rugosa, per tuberculos rugiformes 5 nigros circumscripta, marginibus infero-lateralibus vittam transversa strigatum notatis. Pronoti collum crasse transverse plicato strigatum. Mesonotum crasse cribro-punctatum, haud strigatum. Tegulae rufidæ. Mesopleurae dense punctatae. Scutellum et postscutellum rugulosa, basi et apice polita. Metanotum crassissime foveolato punctatum. Abdominis petiolus ut solitum confertim transverse striolatus. Abdomine de reliquo lævigatum, sericans, basi petiolarum rugulosa. Terebra nigra, annulo ante apicem longiusculo albido. Pedes nigri, politi, partibus rufo-testaceis. Coxæ postice plus minus crasse subsquamoso rugosæ, ac punctatae, superne apice transversæ strigatae. Femora postica subtus crenata, dentibus-que 2 armata. Ungues rufæ. Alæ nebulosæ, venis nigris.

"Long. 19-27; thorax 4.5-6; petioli 6.5-9.5; alæ 10.5-16.5; oviposit. 26.5-34 mm."

M. de Saussure tentatively suggests as males for this species two very small insects, taken in Siam. They differ in having the head entirely red, the occiput almost striate, as in *S. borneensis* Sauss., the sculpture of the body less pronounced, and the pronotum scarcely striate in one specimen. Length 10 mm.

This species appears to closely resemble *S. furcatus* Lep. & Serv., but the face is rugose-punctate, not arcuate rugose; the mesonotum, median segment, and mesopleuræ densely punctate, and the head red. It also resembles *S. coronator* Fab., but differs in the red head and the sculpture of head and mesopleuræ.

Schulz (*l. c.*) alters the name of this species to *saussurei*, on the ground of *ruficeps* being preoccupied by Cameron's Central American insect. As the latter falls into the subgenus *Hemistephanus*, I reinstate the original name.

## 28. CORONATOR Fab.

*Pimpia coronator* Fab. (2), p. 118, ♀. *Stephanus coronator* Boisd., p. 656, pl. 12, fig. 7, ♀; Schlett., p. 114, ♀ ♂; Enderl. (4), p. 306, ♀ ♂. *Megischus cor.* Brull., p. 538, ♀; Sichel (2), p. 477, ♀ ♂. *Megischus insularis* Smith (1), p. 120, ♀ ♂. *Megischus viduus* Smith (2), p. 138, ♂. *Megischus longicaudatus* Costa, Ach. (2), p. 271, ♀ ♂; (1) p. 81, ♀ ♂, pl. iv. figs. 1 a ♂, 1 b ♀.

♀. Face coarsely arcuate rugose; occiput immediately behind tubercles arcuately, behind this centrally transversely, laterally obliquely rugose. Posterior margin of head sharply bordered. Cheeks distinctly longer than scape. Second flagellar joint twice as long as first, third a little longer than second. Neck very coarsely transrugose; semiannular polished, with a few punctures in front. Mesonotum coarsely, densely, and posteriorly partly confluent punctate, anteriorly more diffusely, with a distinct central longitudinal row of punctures and indistinct lateral impressions. Scutellum centrally smooth, lateral lobes diffusely punctate. Mesopleuræ almost smooth and shining above, rugose-punctate beneath; metapleuræ coarsely and densely punctate, separated by a slightly rugose sulcus from the coarsely cribrate punctate median segment. Petiole basally coarsely, apically more finely transrugose, little shorter than remainder of abdomen, which is basally rugose, otherwise feebly shining. Terebra rather longer than body, sheaths white-banded before apex. Hind legs with coxæ coarsely transrugose behind; femora polished smooth and posteriorly extremely finely punctate, bidentate; tibiae much longer than femora, compressed in basal third; tarsi three-jointed.

♂. Similar to ♀ but more slender; petiole is to rest of abdomen as 5: 6; hind tarsi 5-jointed.

Black; head, mandibles except apices and the scape ferruginous; anterior legs chestnut-brown. Wings infumate, with darker spot in middle.

Length 20–40 mm.; males average about 5 mm. less than females.

Habitat: East India; Sarawak; Java; Bachian; Ceram; Amboina; Kaissa; New Guinea; Australia; Sumatra. Dr. Dohrn.

*M. insularis* Smith. Types in British Museum. From Sarawak. Rather small, but typical specimens of *S. coronator* Fab.

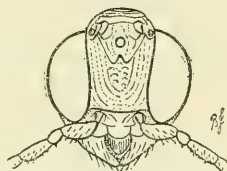
Length ♂, 19 mm.; ♀, 20 mm.; terebra 25 mm.

Text-fig. 2.



*Stephanus coronator.*

Text-fig. 3.



*Stephanus coronator.*

This species greatly resembles *S. ducalis* Westw., from which it may be distinguished by the smooth semiannular and by the sculpture of mesonotum, mesopleuræ, and median segment.

From *S. hæmatipoda* Montrz. it can be known by its red head with less prominent posterior margin, and by the sculpture of head, median segment, and hind coxæ; from *S. sulcifrons* Schlett. it may at once be separated by the absence of the sulcus on vertex and by the white-banded terebral sheaths, which latter character will also distinguish it from the African *S. pachylomerus* Schlett.

29. *DUCALIS* Westw.

*Megischus ducalis* Westw. (4), p. 239, ♀. *Stephanus ducalis* Schlett., p. 112, ♀. *Stephanus lucidus* Szépl., p. 532, ♂.

♀. Frons coarsely transrugose; vertex coarsely arcuate rugose; occiput centrally distinctly impressed, arcuate rugose in front, becoming transverse towards posterior margin of head, which is sharply bordered; cheeks shorter than scape; flagellar joints normal. Neck coarsely transrugose, semiannular less coarsely, with shining smooth posterior margin. Mesonotum centrally smooth, diffusely punctate in front, with a rather indistinct central longitudinal row of punctures and two shallow lateral impressions, laterally and posteriorly coarsely rugose-punctate. Mesopleuræ smooth above, rugose-punctate beneath: metapleuræ coarsely rugose-punctate, separated by a deep transrugose sulcus from the cribrate punctate median segment. Petiole basally irregularly, apically finely and transversely rugose, shorter than rest of abdomen; 2nd segment basally coarsely rugose, its apex and the last segment shining, remaining segments dull. Terebra longer than body, sheaths black, white-banded before the apex. Legs sparsely pubescent; hind legs with coxæ coarsely transrugose, femora smooth and shining in front, finely punctate behind, bidentate; tibiæ longer than femora, compressed not quite to middle; tarsi three-jointed.

Black; head, scape, and base of mandibles ferruginous. Wings infusate, centrally darker.

Length 20–36 mm.; terebra 25–41 mm.

Westwood's type is in the British Museum.

♂. Differs from the ♀ chiefly in the occiput being more obliquely rugose, petiole only basally rugose, 2nd segment basally rugose as in ♀, but remainder of abdomen smooth and shining; hind tarsi five-jointed; anterior femora partly, their tibiæ and all the tarsi often dark red.

Length 20–23 mm. Szépligetti's type (*S. lucidus*, ♂) is in the Hungarian National Museum at Budapest.

Habitat: widely distributed in the Indo-Australian Region; East India, Java, Sumatra, Borneo, Pulu-Penang, Celebes, Sumba, Key Island, Bachian, and New Guinea.

Schulz (2), p. 19, mentions a very large ♀, 36.5 mm., in which the posterior angles of median segment, metapleuræ, petiole, and hind coxæ are all of a metallic steel-blue or violet—colours not previously observed in this family.

This species differs from *S. coronator* Fab. chiefly in the head being impressed behind the vertex; the rugose semiannular, and the coarse sculpture of mesonotum, mesopleuræ, and median segment further distinguish it. From *S. hematipoda* Montrz. it may be known by the impressed head, the arcuately rugose vertex, less prominent posterior border of head, and by the sculpture of the median segment. The absence of the sulcus on vertex and the white-banded terebral sheaths will suffice to separate this species from *S. sulcifrons* Schlett.



## 30. LANCEOLATUS Kieff.

*Stephanus lanceolatus* Kieffer (3), p. 277, ♀.

♀. Head from antennæ to the sharply bordered posterior margin coarsely arcuate rugose; anterior frontal tubercle scarcely larger than the lateral ones, posterior pair smaller, the space between tubercles centrally smooth. Flagellar joints normal. Pronotum elongate, with apical transcarina, posteriorly trans-striate, laterally smooth and shining. Mesonotum and median segment smooth, coarsely and diffusely punctate. Scutellum smooth and shining, coarsely punctate on margins of lobes. Propleuræ nearly smooth; meso- and meta-pleuræ coarsely and diffusely punctate, former anteriorly subrugose. Petiole coarsely and closely trans-striate, as long as rest of abdomen; second segment smooth and shining, four times as long as broad; remainder transverse, shagreened, and shining. Terebra about half as long again as body, sheaths white-banded before apex. Middle and hind coxæ smooth, with whitish pubescence; hind femora smooth, bidentate; tibiæ compressed to middle. Stigma very long and pointed.

Black; head except apices of mandibles, two basal antennal joints, front legs except basal third, and hind tarsi red; intermediate legs black-brown. Wings infumate, distally darker, external median and submedian cells and thence to posterior margin brown; stigma and nervures black.

Length 24 mm.; terebra 37 mm.

Habitat: Obidos on the Amazon (P. Kihler).

Distinguished from *S. maculipennis* Westw., especially by the coarsely trans-striate petiole without lateral tubercles; from *S. ruficeps* Sauss. it may be known by the arcuate rugose head and darker wings.

## 31. HÆMATIPODA Montrz.

*Stephanus hæmatipoda* Montrz., p. 114; Schlett., p. 116, ♀.

♀. Frons coarsely and irregularly rugose, somewhat obliquely near the eyes; occiput arcuate rugose behind the tubercles, posteriorly centrally transrugose, laterally more irregularly. Temples diffusely and finely punctate. Posterior margin of head with slightly reflexed border. Neck very coarsely trans-striate, semiannular smooth, laterally coarsely punctato-rugose. Mesonotum centrally diffusely punctate, with a longitudinal row of conspicuous punctures and indistinct lateral impressions, remainder coarsely and subtransversely rugose-punctate. Scutellum polished smooth with a few marginal punctures. Mesopleuræ smooth above, slightly rugose in front and behind, coarsely rugose-punctate beneath, separated by a deep rugose sulcus from the median segment, which is very coarsely cribrate punctate, laterally and apically indistinctly transrugose. Petiole coarsely, anteriorly irregularly, otherwise distinctly transversely rugose,



a little shorter than remainder of abdomen and as long as hind coxæ, trochanters, and femora together; second segment basally rugose, apically smooth, the remainder dull. Terebra white-banded before apex. Hind legs with coxæ very coarsely transrugose; femora smooth, bidentate; tibiæ much longer than femora, compressed not quite to middle.

Black; cheeks marked with pale red; anterior legs ferruginous, their coxæ black and tarsi pitch-brown; apical inflated part of hind tibiæ ferruginous. Wings strongly infumate, centrally darker.

Length 30 mm.

Habitat: Woodlark Island, New Guinea. Bachian, Jobi Island.

Two specimens of this species are in the Royal Nat. Hist. Museum in Dresden; in both the antennæ are wanting and terebra broken; Montrouzier states the latter is white-banded.

Schletterer considers this species very similar to *S. coronator* Fab. and *S. ducalis* Westw., in both of which the head is red and the sculpture very different.

### 32. ACUTUS Lep. & Serv.

*Megischus acutus* Lep. & Serv., p. 489; Brull., p. 540, ♀. *Stephanus acutus* Schlett., p. 137, ♀.

♀. Frons moderately coarsely arcuately rugose; occiput very coarsely arcuate rugose near tubercles, otherwise irregularly to transrugose. Temples smooth and shining. Posterior margin of head elongate, reflexed collar-like. Cheeks shorter than scape. Basal flagellar joints normal. Neck coarsely transrugose, less distinctly basally; semiannular smooth, with coarse but diffuse punctures. Mesonotum shining, laterally densely, partly confluent punctate, a median longitudinal row of punctures, on each side of which is a smooth space, followed by a row of broad punctures. Scutellum polished, with a few marginal punctures. Mesopleuræ shining, diffusely punctate; metapleuræ densely pubescent, somewhat rugose, separated by an almost smooth sulcus from the median segment, which is cribrate punctate and apically transrugose. Petiole finely trans-striolate, about as long as remainder of abdomen, which is shining, with a few dull spots, due to microscopic sculpture. Terebra a little longer than body, white-banded before apex. Hind legs with coxæ trans-striolate between coarse rugosities; femora smooth, bidentate; tibiæ compressed not quite to middle.

Black; cheeks and mandibles pale marked; anterior legs have a tendency to become brownish. Wings slightly infusate.

Length 21–30 mm.

Habitat: Brazil; Colombia; Kansas, U.S.A.

This species resembles *S. niger* Smith, but has the posterior margin of head reflexed, face arcuate rugose, mesonotum punctate, not rugose, and longer petiole.

33. *VILLOSUS* Kieff.*Stephanus villosus* Kieffer (1), p. 4, ♀ ♂.

♀. Face and frons irregularly and coarsely rugose, space between the tubercles strongly impressed; vertex with three arcuate transcarinae; occiput coarsely and densely longitudinally rugose; posterior margin of head produced into a broad horizontal translucent collar. Second flagellar joint two and a half times as long as first, third more than twice as long as first and second together and about two and a half times as long as second. Prothorax coarsely and rather diffusely transrugose, basally more strongly and more diffusely. Mesonotum smooth, with median line of punctures and laterally transrugose; scutellum with two anteriorly convergent irregular rows of punctures and slightly rugose, anterior lobes diffusely punctate. Mesopleuræ white pubescent, the impressed part transrugose. Metapleuræ and median segment with large and partly confluent punctures, former white pubescent. Petiole finely trans-striate, about as long as rest of abdomen, which is basally striate. Terebra as long as body, sheaths black, white-banded before apex. Hind legs with coxæ finely trans-striate, as long as the bidentate femora; the tibiæ longer than femora, constricted in basal third and compressed beyond middle; tarsi three-jointed, with long grey pubescence beneath.

Shining black; head except apices of mandibles, scape, and second joint of hind trochanters red; anterior legs black-brown. Thorax and legs with long, sparse, whitish pilosity, the hairs on meso- and meta-pleuræ inserted on granular prominences. Wings hyaline.

Length 16 mm.

♂. Similar to ♀, but second flagellar joint not twice as long as first; third shorter than first and second together. Mesonotum red-brown; hind tarsi five-jointed, red, less densely pubescent beneath; genital organs testaceous.

Length 12 mm.

Habitat: Jataneý, Prov. Goyaz, Brazil. Coll. M. de Saule.

The unusual proportions of the basal flagellar joints in ♀ are very characteristic.

34. *RUFOFEMORATUS* Szépl.*Stephanus rufofemoratus* Szépl., p. 532, ♂.

♂. Frons coarsely rugose, vertex transrugose, occiput coarsely rugose; posterior margin of head bordered. Flagellar joints normal. Neck rugose, semiannular smooth, diffusely punctate. Mesonotum coarsely punctate, shining; scutellum smooth and shining. Mesopleuræ closely punctate and shining. Median segment diffusely and coarsely punctate and shining. Petiole only basally rugose, remainder smooth and shining, as long as rest of abdomen. Hind legs with coxæ shining, diffusely rugose; femora smooth, bidentate; tarsi five-jointed.

Black; legs from femora red; basal half of hind tibiæ black. Wings brown, centrally darker; hind wings with indications of cubital and radial nervures.

Length 22 mm.

Habitat: Rubiana, New Georgia, Solomon Islands. Type in the Hungarian National Museum, Budapest.

Easily distinguished by the smooth petiole and red femora.

This species closely resembles *S. rubripes* Morley, from which it differs in the smooth petiole, proportions of basal flagellar joints, the sculpture of semiannular, mesopleuræ, and hind-coxæ.

35. *COMMA* Morley.

*Stephanus comma* Morley (1), p. 105, ♂.

♂. Head semicircularly rugose in front, trans-sulcate below scrôbes. Tubercles small and transverse; vertical carina prominent; occiput trans-striate; posterior margin of head truncately bordered. Antennæ very slender and elongate, 21 mm., second flagellar joint half as long again as first, third half as long again as second, shorter than first and second together. Thorax superficially but confluent punctate, the rather short prothorax transcarinate, its posterior margin smooth. Scutellum smooth, the basal sulcus crenulate. Mesopleuræ longitudinally bisulcate; metapleuræ rugulose, bisulcate above. Petiole minutely transaciculate and apically explanate, shorter than rest of abdomen, which is finely alutaceous and somewhat shining. Hind coxæ (4 mm.) rather shorter than femora (5 mm.), which are bidentate, with four small teeth before the central tooth and another beyond it. Lower nervure of external median cell in fore wing deflexed in the form of a comma at base, apically wanting; hind wing with costal nervure only, emitting a slight spurious nervure from its apex below the three frenal hooks.

Black: head except apices of mandibles, the tubercles and the occiput centrally, base of antennæ, second and fourth segments laterally basally, whole of third segment, anterior legs except coxæ, and apical third of hind femora including the teeth bright brick-red. Hind tibiæ basally black, reliquæ desunt. Wings slightly infumate hyaline; stigma and nervures black; costal and external submedian cells conspicuously darker.

Length 27 mm.; abdomen 18 mm.; petiole 8 mm.

The type was taken by Dr. W. M. Graham "in forest on trunk of tree" at Pbuasi, Ashanti, on 29 May, 1907. In coll. British Museum.

36. *PILOSUS* Elliott (4), p. 256, ♂.

♂. There are sparse white hairs on the head, longer and denser on the petiole and apex of abdomen. The pleuræ are covered with dense white pilosity, and on the legs, the hairs, though less dense, are longer and more conspicuous. Frons,

vertex, and occiput strongly arcuate rugose; one strong carina between the posterior ocelli and two behind them; ocellar space depressed. Posterior margin of head broad and slightly reflexed. Temples with a few setiferous punctures. Second flagellar joint fully twice as long as first; third a little longer than second. Prothorax transcarinate, semiannular smooth and laterally hairy. Scutellum centrally smooth, lateral lobes coarsely rugose-punctate. Metapleuræ and median segment cribrate punctate, separated by a strong carina, which is anteriorly somewhat rugose, posteriorly smooth and shining. Petiole trans-striate, basally more coarsely, shorter than rest of abdomen, which is smooth. Hind coxæ stout, coarsely transrugose; femora smooth, bidentate, the teeth long and acuminate; tibiæ as long as femora and trochanters, strongly compressed in basal third.

Black; head, scape, base, and apex of anterior femora red; frontal tubercles apically black. Wings faintly iridescent; fore wings centrally, hind wings apically infusate; stigma and nervures black-brown.

Length 22 mm.; abdomen  $14\frac{1}{2}$  mm.; petiole 6 mm.

Habitat: Palaboehan, Ratoe. M. E. Walsh (*ex* Frisby), 22 Feb., 1916. Type in coll. Claude Morley.

In the coarse sculpture and conspicuous pilosity, this species much resembles *S. villosus* Kieff.

### 37. *rugosus* Elliott (4), p. 256, ♂.

♂. Frons arcuate rugose; vertex and occiput with strong longitudinal carinæ, occiput regularly, vertex less regularly arcuate striate; three strong carinæ behind posterior ocelli. Posterior margin of head bordered. Cheeks slightly shorter than scape, smooth. Basal flagellar joints normal. Neck transcarinate, semiannular smooth, with a few punctures. Propleuræ finely trans-striate. Mesonotum apically smooth, central row of punctures distinct, the smooth space on each side with a single puncture before and behind, laterally strongly punctate, separated from scutellum by two carinæ. Scutellum centrally smooth, laterally strongly rugose-punctate. Metapleuræ and median segment cribrate punctate, separated by a strong carina. Petiole strongly transrugose, shorter than the remaining smooth segments. Hind coxæ coarsely trans-striate; femora smooth, bidentate; tibiæ slightly longer than femora, compressed to middle.

Black; head, except apices of mandibles, and apex of thorax above red; anterior legs more or less rufescent. Wings hyaline.

Length 16 mm.; abdomen 10 mm.; petiole  $4\frac{1}{2}$  mm.

Habitat: Java; Preanger Regency, near Seekoboemi. M. E. Marsh, 1918. Type and co-types in coll. Claude Morley.

This species bears a superficial resemblance to both *S. unicolor* Schlett. and *S. ducalis* Westw., but differs considerably in sculpture.



## 38. VIOLACEIPENNIS Cam.

*Megischus violaceipennis* Cameron (2), p. 225, ♀.

"Niger; pedibus rufis; coxis, trochanteribus, femoribus posticis basique tibiæ posticarum nigris; alis fusco-violaceis, nervis nigris. ♀.

Long. 24 mm.

Antennæ black, slender. Front rugosely punctured above; the sides above stoutly obliquely, the lower part transversely striated, the ocellar region irregularly reticulated, the keels above them mostly curved; above the reticulated upper portion are four long curved keels, the vertex behind them is irregularly rugosely striated; the ocellar region is distinctly depressed; the three tubercles form a triangle. The base of the pronotum is smooth and shining; behind on the sides are two stout curved keels; the rest of the pronotum is opaque and irregularly transversely striated. The base of the mesonotum is smooth and shining, the rest of it bears mostly large and deep punctures, except a space on either side of the centre; on the sides and base the punctures tend to become confluent. Scutellum somewhat triangular in shape, smooth, shining and impunctate. Median segment closely, stoutly irregularly punctured; behind, the punctures run into reticulations. Propleuræ smooth and shining; the mesopleuræ opaque, irregularly punctured, and striated; the metapleuræ rugosely punctured. The four front legs are rufous, with the coxæ darker; the hinder black, except the apical two-thirds of the tibiæ and the tarsi, which are rufous at the base, blackish towards the apex; the hind coxæ are, as usual, irregularly striated; the two teeth on the hind femora are acute; the apical one is longer and narrower than the hinder. Wings fusco-violaceous; the nervures and stigma are black. The petiole is longer than the rest of the abdomen united; it is opaque and closely striated. The ovipositor is annulated with white and is not quite as long as the body. The recurrent nervure in the fore wing is interstitial."

Habitat: New Britain (Dr. Arthur Willey). Type in Cambridge Museum.

Said by Cameron to be very like his *S. froggattii*, but, in the absence of details as to the posterior border of head and relative length of the basal antennal joints, I am unable to place it definitely in my table.

## PARASTEPHANELLUS Enderl.

In the (2) Zool. Anz. xxxiii. pp. 453-475, Dr. Gunther Enderlein erects a new subgenus, *Parastephanus*, which he defines as having that part of the median nervure beyond the outer submedian cell obsolete, and the cell consequently open behind, the size of the discoidal cell and the breadth of the stigma being variable. He thus includes species from the Indo-Australian and Neotropical Regions.





- (28.) 27. Frons trans-striate; intertubercular space unusually long.  
14. *claripennis* Cam.  
(27.) 28. Frons rugose.  
(32.) 29. Frons rugose punctate.  
(31.) 30. Neck of pronotum strongly trans-striate; median segment  
punctate ..... 15. *rufo-ornatus* Cam.  
(30.) 31. Neck longitudinally striate; median segment reticulate rugose.  
16. *rubripictus* Elliott.  
(29.) 32. Frons rugose but not punctate; metapleuræ smooth; median  
segment diffusely punctate ..... 17. *malayanus* Cam.

# 1. MARTINI Stadlm.

*Stephanus martini* Stadelmann (1), p. 236, ♀ ♂.

♀. Frons transrugose, coarsely punctate below; occiput coarsely transrugose; posterior margin of head sharply bordered. Basal flagellar joints normal. Neck coarsely and obliquely rugose; semiannular coarsely punctate with polished posterior margin. Mesonotum diffusely punctate. Scutellum smooth, with a few diffuse marginal punctures. Mesopleuræ shining, apically punctate; metapleuræ densely punctate, separated by a deep and shining sulcus from the coarsely cribrate-punctate median segment. Petiole basally longitudinally, apically transversely rugose, and as long as the remaining segments together; apical segments dull. Terebra very little longer than body, sheaths entirely black. Hind coxæ transrugose; hind femora finely trans-striate and tridentate; tarsi three-jointed.

Black; head, scape, and first flagellar joint red; anterior legs nigro-fuscous; all tarsi testaceous. Wings subhyaline.

♂. Similar to ♀. Nigro-fulvous, head red, antennæ basally red, apically nigro-ferruginous; base of hind femora ferruginous; tarsi five-jointed. Length, ♀, 17–20 mm.; ♂, 15 mm.

Habitat: Dele, Sumatra. Named after the captor, Hofrat Dr. med. L. Martin. Type in Berlin Museum.

Stadelmann states that this species closely resembles *S. sulcifrons* Schlett., which has the neuration of the subgenus *Stephanus*; he states also that the neuration is complete, but his figure (*l. c.* pl. 6. fig. 4) shows the external submedian cell open behind as in *Parastephanellus*.

Other differences are said to be: the sulcus on vertex indistinct in ♀, wanting in ♂; third flagellar joint longer, petiole longer and more coarsely sculptured; hind femora trans-striate and tridentate, but smooth and bidentate in *sulcifrons*.

Easily known by the tridentate hind femora and large size.

# 2. ORBITALIS Brues.

*Parastephanellus orbitalis* C. L. Brues, p. 98, ♂.

♂. Frons and vertex centrally transrugose; cheeks longer than scape; posterior margin of head bordered but not reflexed. Basal flagellar joints normal. Pronotum transrugose, the rugosities extending obliquely to the pleuræ; a punctate area on each side before the smooth posterior margin. Mesonotum

sparsely foveate punctate, with punctate median line; scutellum smooth, with coarse lateral punctures. Mesopleuræ pubescent in front, smooth and shining behind; metapleuræ irregularly rugose. Median segment with diffuse, large, and shallow punctures, separated from the metapleuræ by a smooth sulcus and a reticulate ridge. Petiole two-thirds as long as thorax, trans-striate above, irregularly rugose laterally and below; remaining segments polished. Claspers short, basally smooth, apical half punctate and hairy, apex rounded, with dense fringe of short hairs. Hind coxæ trans-striate, with a smooth area externally near the base. Hind femora tridentate.

Black; face to just above antennæ and inner orbits narrowly pale yellowish, outer orbits more widely above white. Palpi and antennæ piceous, base of flagellum fuscous; propleuræ below rufous; front legs anteriorly brown-yellow; all knees and apices of tibiæ are whitish, all tarsi honey-yellow. Wings slightly infusate; stigma about half as wide as radial cell, petiole of discoidal cell short.

Length 7-8 mm.

Habitat: Fulkora, Solomon Islands (F. W. Mann). Type and paratype in the Museum of Comparative Zoology at Harvard College, U.S.A.

The black head and the sculpture of pronotum and median segment will distinguish this species from the only other of similar size with tridentate hind femora (*glaber* Elliott).

### 3. GLABER Elliott.

*Parastephanellus glaber* Elliott (2), p. 129, ♀.

♀. Frons arcuate rugose, vertex strongly transrugose, occiput becoming gradually smoother towards the slightly raised posterior margin, and with distinct longitudinal impression; carinæ between the posterior ocelli very inconspicuous, scarcely to be distinguished from the transverse striæ; anterior frontal tubercle very prominent. Cheeks shorter than scape; basal flagellar joints normal. Prothorax glabrous. Neck rather short; mesonotum smooth; scutellum with marginal punctures only; pro- and meso-pleuræ very finely alutaceous, metapleuræ almost smooth and median segment with scarcely any visible sculpture. The pleuræ, abdomen beneath, and the legs with erect white hairs. Petiole very finely trans-striate, slightly longer than rest of abdomen, which is smooth. Terebra longer than body, sheaths black. Hind legs with coxæ finely trans-striate, femora smooth, tridentate; tibiæ compressed to middle.

Black; head rufescent, with white line under eyes as in *P. damellicus* Westw.; a testaceous mark on frons just below the anterior tubercle, which is pale rufescent. Legs rufescent, base and apex of tibiæ paler and all metatarsi whitish.

Length 8 mm.; abdomen  $4\frac{1}{2}$  mm.; petiole  $2\frac{1}{2}$  mm.; terebra 11 mm.

Habitat: Singapore. "F. Sm. Coll."

The almost entire absence of visible sculpture is characteristic.

The colour of head and legs and the sculpture will easily distinguish *P. orbitalis* Brues, which is the only other species of similar size with tridentate hind femora.

#### 4. PYGMÆUS Enderl.

*Stephanus pygmæus* Enderl. (1), p. 197, ♀ ♂. *Parastephanellus pygmæus* Enderl. (2), p. 472 *et seqq.*; (4), p. 289 *et seqq.*

♀ ♂. Frons extremely finely and densely punctate; all five frontal tubercles acuminate, the posterior pair smaller; vertex and occiput obsoletely transaciculate; posterior margin of head sharply bordered. Antennæ very slender, second flagellar joint scarcely one and a half times as long as first; third shorter than first and second together. Neck almost smooth, its posterior margin polished. Mesonotum rugose; scutellum polished smooth; metanotum (the small visible part of the true metanotum) longitudinally striate. Mesopleuræ smooth, pubescent, diffusely punctate in front only; metapleuræ coarsely and deeply rugose, separated by a shining smooth space and a row of punctures from the densely punctate median segment. Petiole finely rugose and shorter than the remaining segments together. Terebra about two-thirds of the length of body; spicula red-brown, sheaths entirely black. Legs covered with fine erect hairs, hind femora bidentate.

Yellow-brown; apical two-thirds of antennæ, apex of mandibles, meso- and meta-thorax, pleuræ and median segment darker, yellow-brown to black-brown. Wings hyaline, external submedian cell infumate; stigma short and broad, dark brown.

Length, ♀, 7-8 mm.; ♂, 5-7 mm.

Seven ♂ ♂ and 3 ♀ ♀ in Berlin Zoological Museum; collected by Nicholitz at Milne Bay, New Guinea.

Dark specimens of the present species greatly resemble lighter ones of *P. damellicus* Westw., also from New Guinea, but are easily known by the shorter and broader stigma, infumate spot in wing, shorter petiole, and, in ♀, shorter terebra.

#### 5. LÆVICOLLIS Morley.

*Parastephanellus lævicollis* Morley (1), p. 111, ♀ ♂.

♀. Head finely and evenly trans-striate; vertex coarsely transcarinate; posterior margin of head bordered; cheeks smooth and a little longer than scape. Second flagellar joint half as long again as first; third half as long again as second. Neck very short and smooth, semiannular smooth, with a few fine punctures, as is also the mesonotum. Scutellum quite smooth and separated from mesonotum by crenulated lines. Mesopleuræ and metapleuræ obsoletely shagreened, not punctate, the latter separated from metanotum by a basally obsolete carina. Median segment centrally smooth, apically rugulose, and basally with a few



large punctures. Petiole very finely transaciculate, shorter than the remaining segments, which are smooth; second segment basally somewhat elongately attenuate. Terebra longer than body, sheaths entirely black. Hind coxæ transaciculate, their femora smooth with a few setiferous punctures, bidentate; tibiæ longer than femora, constricted to middle.

Black; antennæ and palpi infusate; base of antennæ, mandibles except apices, clypeus and frons fulvous; face and whole external orbits and all tarsi whitish. Wings hyaline, stigma and nervures piceous.

♂ differs in having the whole head except the whitish external orbits dull red; base of occiput nitidulous; basal flagellar joints longer, though in the same proportions; propleuræ dull testaceous; anterior femora and tibiæ piceous.

Length 9 mm.; abdomen 5 mm.; petiole 2 mm.; terebra in ♀ 11 mm. A single pair, now in British Museum, taken in the Ding-Ding Island in the Indian Ocean during 1896 and 1900.

#### 6. ALBICEPS Elliott.

*Parastephanellus albiceps* Elliott (2), p. 130, ♀.

♀. Frons subarcuate striate, the striæ broken into granules, vertex and occiput finely granulate striate; second flagellar joint one and a half times as long as first, third slightly shorter than first and second together. Pronotum very finely trans-striate throughout, neck very short; mesonotum subglabrous; scutellum normal; propleuræ finely, obliquely striate; mesopleuræ alutaceous; metapleuræ punctate, separated by a deep crenulated sulcus from the alutaceous and punctate median segment. Petiole trans-striate, shorter than the rest of the smooth abdomen. Terebra rather shorter than body, rufescent, apically black. Hind legs with coxæ trans-striate, femora finely alutaceous, bidentate; tibiæ compressed to middle.

Black; mandibles basally flavous, all orbits broadly white; antennæ basally, anterior legs except middle coxæ rufescent, hind tibiæ and tarsi much paler. Wings hyaline; stigma and nervures brown.

Length  $9\frac{1}{2}$  mm.; abdomen  $5\frac{1}{2}$  mm.; petiole  $2\frac{1}{2}$  mm.; terebra  $8\frac{1}{2}$  mm.

Habitat: Victoria, Australia. R. E. Turner, 1907.

Easily known by the extremely broadly white orbits.

#### 7. MACULIFRONS Cam.

*Megiseleus maculifrons* Cam. (3), 1902, p. 32, ♂.

♂. Frons closely punctate; vertex and occiput transrugose; posterior margin of head bordered. Second flagellar joint twice as long as first, third shorter than first and second together. Prothorax short, nearly smooth and shining, neck with a transverse carina; mesothorax closely and finely punctate, dull;



scutellum smooth. Mesopleuræ nearly smooth; metapleuræ transrugose, separated by a sulcus from the cribrate-punctate median segment. Petiole trans-striate, longer than rest of abdomen, which is feebly shining, discally depressed. Hind legs with coxæ trans-striate above; femora alutaceous, shining, bidentate; tibiæ constricted to beyond middle.

Black; head red, upper part of frons, the vertex, and occiput black, with a broad red mark behind the posterior ocelli; outer orbits yellowish; scape and basal flagellar joint rufous. Wings subfuscous, nervures black.

Length 12 mm.

Habitat: Baram District, Low Country, Sarawak. Robt. Shelford. Type in British Museum.

The peculiar generic name "*Megiseleus*" appears to be a printer's error. If the writing were indistinct, the "ch" might easily be mistaken for "ele."

#### 8. EBURNEUS Morley.

*Parastephanellus eburneus* Morley (1), p. 35, ♀ ♂.

♀. Frons rugose, trans-striate. The three anterior frontal tubercles acuminate, front one longest and recurved; posterior pair smaller and rounded. Occiput finely trans-striate. Posterior margin of head bordered. Second flagellar joint one and a half times as long as first; third shorter than first and second together. Neck short, smooth, and shining; semiannular finely rugose. Mesopleuræ obsoletely trans-striate and dull; metapleuræ smooth and shining, separated by a deep sulcus from the median segment, which is smooth, with large, diffuse punctures. Petiole with basal half finely trans-striate, longer than remainder of abdomen, which is dull and obsoletely punctate. Terebra shorter than body, sheaths black. Hind legs with coxæ obsoletely transaciculate; femora nearly smooth and shining, bidentate; tibiæ compressed to middle.

Black; face, clypeus, mandibles except apically, and a streak at the inner orbits testaceous white; a broad stripe from base of mandibles to near occiput ivory-white; scape and basal flagellar joint testaceous; base and apex of intermediate tibiæ white. Wings clear hyaline, stigma pale.

Length 6 mm.; terebra 5 mm.

♂. Similar to ♀; petiole piceous, genital valvulæ testaceous.

Length  $3\frac{1}{2}$  mm.

The ♀ was taken by O. S. Wickwar at Candy, Ceylon, Feb. 1910; the ♂ by Green, on a leaf infested by a Coccid, *Hemichionaspis brasiliensis*, at Pradenula, Ceylon, June 1909. Types in British Museum.

Similar to the Australian *P. rufo-ornatus* Cam., ♂, but the petiole is longer, the sculpture of median segment is different, and the coloration is very distinctive.

9. *DAMELLICUS* Westw.

*Stephanus damellicus* Westw. (5), p. 126, pl. xxiv. fig. 2; Schlett., p. 116, ♀. *Hemistephanus damellicus* Morley (1), p. 112. *Parastephanellus d.* (2), p. 29, ♀.

Westwood's original description is as follows:—

"Niger; capite et antennarum basi piceo-rufis; pedunculo abdominis pedibusque rufis; capite antice trituberculato verticeque carina parva transversa instructo, linea tenui alba utrinque sub oculos; antennis gracillimis, pone medium fuscis; collari trigonotruncato, collo lævi, metanoto basi serie striolarum brevissimarum notato, pedunculo abdomen longitudine æquanti, transversim lævissime striolato; abdomine ovali nitido, oviductu longitudine caput et corpus totum æquanti; pedibus posticis crassis, coxis elongatis transversim carinatis, femoribus clavatis, subtus serratis dentibusque tribus majoribus armatis; tibiis pone medium subito dilatis; tarsi posticis 3-articulatis; alis hyalinis venis distinctis nigris, stigmatum nigro basi lutescenti.—*Hab.* Austral. In Mus. Hopeano Oxoniæ.

"The mandibles are robust, their inner margin (seen from above) has two obtuse teeth, seen laterally they are more irregular. The marginal cell is slightly open at the tip, the vein forming the hinder margin of the incomplete second submarginal cell is abbreviated, and the second discoidal cell is incomplete, the vein forming its hinder margin being obsolete.

"Species proxima *Stephanus hæmatipoda* Montrouzier, Ann. Soc. Agric. Lyon, T. vii. 1, p. 113. *Hab.* Woodlark Island."

Having examined the beautifully preserved type, I am able to correct and complete the above description.

Frons anteriorly rugose-punctate, transrugose above, vertex with a very conspicuous transverse carina, behind which the head is arcuate rugose, becoming trans-striate towards the strongly bordered posterior margin. The three anterior tubercles very prominent, the two posterior subobsolete. Antennæ very slender; basal flagellar joints normal. Neck smooth, semiannular transrugose. Mesonotum coarsely but not closely rugose-punctate; metanotum (the small strip visible) longitudinally striate. Mesopleuræ finely punctate; metapleuræ punctate and separated from the rugose median segment by a line of punctures. Petiole finely striate throughout, slightly shorter than remainder of abdomen, which is smooth and shining. Terebra slightly shorter than body. Hind legs with coxæ strongly trans-striate; femora bidentate; tibiæ compressed to slightly beyond the middle. Black; the anterior tubercles and the carina on vertex are bright red, remainder of head and base of antennæ dull red, with a broad white line on each side, starting from the posterior margin, passing under the eyes, and meeting over the mouth. Neck of pronotum, mesonotum partly, petiole, and legs red. Wings hyaline, stigma rufescent, basally paler, nervures black.

Length  $8\frac{1}{2}$  mm.; abdomen 5 mm.; petiole 2 mm.; terebra 8 mm.

The "carina parva transversa" is unusually large, and its bright red colour makes it very conspicuous. The small visible portion of the true metanotum is longitudinally striate, but the median segment is rugose. The hind femora are furnished in the anterior half beneath with two comparatively long and very sharp spine-like teeth, and can only be called bidentate. There is a slight blunt projection near the base, more pronounced on the right femur than on the left, but these do not count as teeth. The white line on the head, extending, as one might say, from ear to ear, is very characteristic.

Enderlein ((1), p. 196) describes both sexes of a *Parastephanellus*, which he considers to be identical with the present species, differing in colour only. The neck coarsely longitudinally striate, the semiannular slightly rugose in front, smooth behind; the petiole as long as remainder of abdomen and apically smooth. No mention is made of the conspicuous carina on vertex, nor of the white line on head, also petiole and legs are differently coloured. They are closely-allied species, but that of Westwood comes from Australia, whereas Enderlein's was taken in New Guinea, Bismarck Archipelago, and Borneo. For this species—*rubripictus* Elliott—see p. 759.

The measurements given by Westwood in lines are approximately correct, and the petiole, remainder of abdomen, and terebra appear to be of equal length. Accurate measurements show slight differences, which may be ignored for purposes of identification, as in my table.

The present species is closely allied to, and may even be identical with *P. pictipes* Roman.

The British Museum has of this species 7 ♀♀, taken by R. E. Turner at Mackay, Queensland, and 1 ♀ from the Swan River. They vary in size from  $6\frac{1}{2}$  mm., terebra 7 to 13 mm., terebra  $14\frac{1}{2}$  mm. The only difference from the type is in the slightly longer terebra, which is shorter than the body in the type but longer in these. I do not consider this sufficient to create a new species.

#### 10. *PICTIPES* Roman.

*Parastephanellus pictipes* Roman (1), p. 1, ♀.

♀. Head seen laterally scarcely higher than long. Frons strongly but scarcely transversely rugose; the five tubercles rather prominent but obtuse, the vertex behind them furnished with a short carina; occiput towards base more coarsely and more transversely striate, with indistinct longitudinal impression; posterior margin of head emarginate, not bordered. Antennæ short, scarcely reaching beyond thorax, 23-jointed; pedicellus sub-elongate, half as long as scape; first flagellar joint scarcely longer than scape, second one and a half times as long as first;

third and fourth of equal length and little longer than second. Thorax sub-depressed, pronotum closely and finely trans-striate, neck apically deeply emarginate and bifoveolate. Mesonotum coarsely rugose-punctate, with anterior central longitudinal line of punctures, a strongly crenulate line before scutellum, which is rugose, apically subglabrous, alutaceous. Mesopleuræ tumid, scabrous, with broad and smooth posterior margin; metapleuræ prominent, irregularly scabrous. Sternum smooth and shining, very finely trans-striolate, the punctate mesolecus open behind. Median segment depressed, coarsely rugose-reticulate, basally laterally more finely sculptured. Petiole about as long as remainder of abdomen, centrally slightly incrassate, trans-striate, with smooth apical margin; second segment half as long as first, shining, microscopically reticulate; remaining segments transverse, third to seventh finely and closely trans-striolate, eighth exserted, coriaceous. Apical margins of ventral segments sparsely pale pubescent; hypopygium apically compressed and subacuminate. Terebra shorter than body, sheaths black. Hind legs with coxæ trans-striolate inside; femora bidentate, reticulate, basally externally smooth and shining; tibiæ reticulate, half as long again as femora, with a central, shining, acute-angled impression behind (? constricted to middle and there impressed). Wings extending beyond apex of petiole; in fore wing, stigma nearly five times as long as its breadth, costa not extending beyond it; in hind wings the costa extends to within a third of the apex of wing.

Black; basal half of flagellum, a straight line on cheeks from base of mandibles, touching the eyes, to the temples—not reaching the posterior margin of temples—apices of coxæ, trochanters partly, extreme base and apex of anterior femora, anterior tibiæ chiefly, posterior tibiæ basally, and all tarsi red; intermediate tarsi basally white. Wings hyaline, stigma and nervures black, former basally narrowly pale; radix rufescent, tegulæ nigro-fuscous.

Length 10–11 mm.; terebra 9·5 mm.

Taken by Dr. E. Mjöberg's Swedish Scientific Expedition to Australia, at Derby, Kimberley Division, West Australia, Oct. 1910. 1 ♀.

This is possibly a dark form of *P. damellicus* (Westw.), Enderl., as both have the same unusual streak of colour on the cheeks. But Westwood describes his species as having three large teeth on the hind femora, whereas the present species has only two. Enderlein (Arch. Naturg. 1901) describes a supposed *damellicus* Westw., from New Guinea, the Bismarck Archipelago, and Borneo, which has two femoral teeth but not the long pale streak on cheeks, and also differs from *pictipes* in the sculpture of the pronotum. The present species is now the only *Parastephanellus* in the Stockholm Museum; the nearest species with which it might be compared is the somewhat unlike *Hemistephanus texanus* Cresson. A detailed description has been given so that this species may in future be clearly understood.



Westwood's incorrect description of his *damellicus* as having the hind femora tridentate has caused much confusion. The present species appears to differ chiefly in the five frontal tubercles being prominent, posterior margin of head not bordered, and pronotum somewhat differently sculptured. The peculiar coloration of the head points to close connection between the two, but I do not venture to synonymize them for the present.

#### 11. BREVISTIGMA Enderl.

*Parastephanellus brevistigma* Enderl. (3), p. 203, ♂.

♂. Frons finely arcuate transrugose; the three anterior frontal tubercles acuminate, the two posterior flatly rounded; vertex with three trans-carinae, the space between them polished; occiput finely and closely trans-striate. Antennæ slender and about 25-jointed. Pronotum finely trans-striate, its lateral angles sharply transrugose, posterior margin polished smooth, neck short. Mesonotum coarsely rugose-punctate; scutellum smooth. Mesopleuræ smooth, very finely striate; metapleuræ smooth, reticulately punctate in front above, separated by a row of deep punctures from the median segment, which is coarsely, but not reticulately punctate. Petiole slender, finely and irregularly transrugose, about as long as remainder of abdomen. Hind coxæ finely trans-striate, often granulate; femora bidentate.

Head clear ochre-yellow, vertex slightly nigrescent; apical two-thirds of antennæ brown; prothorax ferruginous, posterior half black above; remainder of thorax, abdomen, hind coxæ, femora, and tibiæ black. Base of second segment and whole of anterior legs ferruginous. Wings hyaline, faintly infusate; stigma  $\frac{3}{4}$  mm. long, and, like the nervures, brown.

Length 6.4 mm.; abdomen 3.9 mm.; petiole 1.9 mm.; fore wing 4.4 mm.

Habitat: Hankau (Koshun), Formosa; 28th April, 1912. Type in Dahlen Museum. (H. Sauter.)

#### 12. PALLIDITARSIS Cam.

*Megischus palliditarsis* Cam. (8), p. 56, ♀. *M. ruficollis* Cam. l. c. p. 57, ♂.

♀ ♂. Frons closely subarcuate trans-striate; vertex more finely trans-striate and occiput nearly smooth. Three frontal tubercles short and bluntly rounded in ♀, more pointed in ♂. Posterior tubercles distinct, but broad and blunt. Posterior margin of head simple. A strong carina between the posterior ocelli and two smaller ones behind it. Second flagellar joint a little longer than first and about as much shorter than third. Pronotum, pro- and meso-pleuræ smooth; scutellum smooth, with a few diffuse punctures; the bordering furrows weakly crenulated in ♀, smooth in ♂. Metapleuræ smooth in ♀, slightly aciculated in ♂. Petiole closely trans-striate throughout, longer than rest



of abdomen, which is smooth. Hind legs with coxæ closely trans-striate, femora smooth and bidentate; tibiæ constricted to beyond middle in ♀, not quite so far in ♂. Terebra in ♀ longer than body.

♀. Black: head rufo-testaceous, outer orbits broadly white, propleuræ and prosternum rufous, base of second segment and the anterior legs rufo-testaceous; middle tibiæ basally broadly, apically narrowly white; hind legs black. Front tarsi partly, middle tarsi entirely, and hind metatarsus except at apex white.

♂. Similar to ♀, but head darker red, face and oral region pale; prothorax entirely red, basal antennal joints paler, anterior legs testaceous, femora darker, hind legs black with knees rufous, constricted part of tibiæ and all tarsi white. Wings, in both sexes, hyaline, nervures and stigma rufous in ♀, darker, with pale base to stigma in ♂.

Length, ♀, 6 mm.; abdomen  $3\frac{1}{2}$  mm.; petiole 2 mm.; terebra 9 mm. Length, ♂, 7 mm.; abdomen  $3\frac{1}{2}$  mm.; petiole 2 mm.

There is no doubt that the two species of Cameron are ♂ and ♀ of the same. His statement that the hind femora of *M. ruficollis* are trans-striate is an evident mistake for coxæ. There are few things more deceptive than the relative proportions of petiole and rest of abdomen. Cameron gives the petiole in this species as "twice longer"; the actual measurements are 2 and  $1\frac{1}{2}$  mm.

Habitat: Kuching, Borneo. John Hewitt. Types in British Museum.

### 13. *scitus* Elliott.

*Parastephanellus scitus* Elliott (2), p. 163, ♂.

♂. Frons strongly arcuate striate, vertex and occiput trans-striate, posterior frontal tubercles subobsolete, two carinæ between the posterior ocelli; posterior margin of head bordered. Scape longer than cheeks; second flagellar joint one and a half times as long as first; third rather longer than second. Pronotum trans-striate, the extreme base smooth, neck short; mesonotum finely punctate; scutellum normal; propleuræ obliquely striate; mesopleuræ smooth; metapleuræ coarsely punctate and separated by a sulcus from the closely and finely punctate median segment. Petiole finely trans-striate, as long as rest of abdomen, which is smooth and shining. Hind coxæ coarsely, their femora finely trans-striate, the latter somewhat strongly inflated, bidentate; tibiæ compressed to a little beyond middle.

Black; head dark red, antennæ pale rufescent, becoming gradually darker towards the apex; extreme base of pronotum, front legs, middle tibiæ and tarsi, hind tarsi, and base of second segment rufescent. There is a scarcely noticeable paler line under the eyes. Wings hyaline, slightly iridescent; stigma rufescent, basally pale; nervures blackish.

Length 8 mm.; abdomen 5 mm.; petiole  $2\frac{1}{2}$  mm.

Habitat: Pusa, Bengal. (T. B. F.) 21.vi.11.

This is the first specimen of this subgenus I have seen from India proper, all the others being from more southern localities; one from Ceylon, one from Ding-Ding Island in the Indian Ocean, and several from Borneo and Australia. It differs from all other males yet described in the sculpture of the head and hind legs, and in colour.

The males are decidedly rarer than the females, and the mate of this species should be discovered ere long.

#### 14. CLARIPENNIS Cam.

*Megischus claripennis* Cam. (8), p. 56, ♀.

♀. Frons finely and closely transrugose, vertex subarcuate striate, occiput finely striate, almost smooth behind. The anterior frontal tubercle longest, and separated from the next pair by a greater distance than these are from each other, the enclosed space being unusually elongate. Three carinæ between the posterior ocelli, the front one strongest. Posterior margin of head strongly bordered. Second flagellar joint half as long again as first; third longer than second, but shorter than first and second together. Pronotum entirely smooth and shining; mesonotum shagreened, and with longitudinal furrow; scutellum elongate and smooth. Propleuræ smooth; mesopleuræ aciculate; metapleuræ obliquely striate. Median segment strongly reticulate punctate. Petiole longer than rest of abdomen, closely trans-striate; remainder of abdomen smooth. Terebra half as long again as body, sheaths black. Hind coxæ closely trans-striate; hind femora smooth, bidentate, their tibiæ compressed to a little beyond middle.

Black; the outer orbits broadly, the anterior tarsi and the middle tibiæ testaceous, hind metatarsus basally white; head rufo-testaceous, vertex blackish, four basal antennal joints pale rufo-testaceous; the second segment basally rufous. Wings clear hyaline; stigma and nervures almost black.

Length 8 mm.; abdomen  $3\frac{1}{2}$  mm.; petiole 2 mm.; terebra 13 mm.

Habitat: Kuching, Borneo. John Hewitt, B.A. Type in British Museum.

#### 15. RUFO-ORNATUS Cam.

*Stephanus rufo-ornatus* Cam. (5), p. 45, ♂. *Parastephanellus rufo-ornatus* Elliott (1), p. 92, ♂. *P. rufid-ornatus* Morley (1), pp. 35 et 112, ♀ ♂.

♂. Frons closely, rugosely, and almost reticulately punctate; vertex closely trans-striate; arcuate striæ between frontal tubercles, and a distinct central longitudinal sulcus on vertex. Second flagellar joint one and a half times as long as first. Pronotum short, finely and closely trans-striate. Mesonotum coarsely rugose; scutellum smooth, with two short lateral

impressions at apex, between which it is striate. Pro- and meso-pleuræ obscurely striate; apical half of metapleuræ irregularly reticulate. Median segment finely and closely punctate, apically centrally striate. Petiole finely and closely trans-striate, as long as rest of abdomen. Hind femora bidentate.

Black; a broad yellow line from base of antennæ to beyond eyes; mandibles pale yellow; antennæ, frontal tubercles, scutellum, apex of petiole, anterior legs, hind coxæ partly, trochanters, apices of femora, the tibiæ and tarsi rufous. Wings clear hyaline; stigma fuscous, basally pale; nervures brown. Abdomen from second segment sometimes red.

Length 5–10 mm.

♀. Similar to ♂. Petiole slightly shorter; terebra longer than body.

Length 13–14 mm.; abdomen  $8\frac{1}{2}$  mm.; petiole 4 mm.; terebra 15 mm.

Habitat: ♂. Burnett River, Queensland (R. Semon); Kuranda, Queensland (Dodd), var. Kuranda, 1904. ♀. Mackay, Queensland; Swan River, West Australia.

The ♀♀, together with the ♂♂ from Kuranda, are in the British Museum.

Easily distinguished from *P. brevistigma* Enderl. by the sculpture of metapleuræ and median segment, and by the colour.

#### 16. RUBRIPICTUS Elliott.

*Stephanus damellicus* Enderl. (nec Westw.) (1), p. 196, ♀ ♂. *Parastephanellus rubripictus* Elliott (1), p. 129, ♀ ♂.

♀ ♂. Frons rather coarsely rugose-punctate, laterally transrugose; the three anterior tubercles very acuminate, posterior pair small; vertex and occiput transrugose; posterior margin of head sharply bordered. Antennæ very slender; basal flagellar joints normal. Neck coarsely longitudinally striate; semiannular feebly rugose, with polished posterior margin. Mesonotum diffusely and coarsely rugose-punctate. Scutellum centrally smooth, with marginal puncturation. Metanotum longitudinally striate. Mesopleuræ pubescent, finely and diffusely punctate; metapleuræ separated by a row of punctures from the coarsely and reticulately rugose median segment. Petiole finely rugose, apically more or less smooth, as long as the remaining segments together. Terebra in ♀ as long as body, spicula red-brown, sheaths black. Legs finely pubescent; hind coxæ densely transrugose; hind femora bidentate, their tibiæ compressed almost to middle.

Black; face, mandibles except apices, cheeks, 4 or 5 basal antennal joints, anterior legs and hind tibiæ red-brown; petiole and hind femora sometimes brownish or rufescent. Wings clear hyaline; stigma long and narrow, brown.

Length, ♀, 11–12 mm.; ♂, 6–11 mm.

Habitat: Milne Bay (Micholitz); Bismarck Archipelago (Dr. Dahl); Borneo (Grabowsky).

This species is distinguished from all others in this subgenus by the long and narrow stigma; from *P. pygmaeus* Enderl. it differs also in the longer basal flagellar joints and entirely hyaline wings.

Enderlein (*l.c.*) considers this species to be merely a dark variety of *P. damellicus* Westw. The sculpture of the pronotum is entirely different, the petiole and hind legs are black, the characteristic white line on face is wanting, and the stigma is longer and narrower. These points, taken in conjunction with the different localities, appear to justify me in regarding them as separate species.

#### 17. MALAYANUS Cam.

*Stephanus malayanus* Cameron (6), p. 43, ♀.

♀. Frons closely and coarsely transrugose; vertex arcuate striate. Anterior frontal tubercle very large; temples broad and inflated. Second flagellar joint half as long again as first. Pronotum striate at apex of basal fovea; propleuræ smooth above, closely striate beneath; mesopleuræ nearly smooth; meta-pleuræ apically coarsely reticulate. Scutellum smooth, with large basal transverse fovea, from which two lines of foveate punctures run to apex. Median segment smooth, with large diffuse punctures. Petiole closely trans-striate, as long as remainder of abdomen. Terebra slightly longer than body, sheaths black. Hind coxæ irregularly trans-striate; hind femora bidentate.

Black; outer orbits, front tubercle, face, frons, and scape more or less obscurely red; anterior legs brown, their tarsi paler; basal joints of hind tibiae testaceous. Wings clear hyaline; stigma and nervures black.

Length 11 mm.; terebra 12 mm.

Habitat: Mankwari, New Guinea (May).

Cameron states that this species much resembles *P. maculifrons* Cam., from Borneo, but is more slenderly built, with hyaline wings and a fovea at base of scutellum, *maculifrons* having the wings infumate, no fovea at base of scutellum.

#### HEMISTEPHANUS.

Enderlein (4), pp. 189 et 301.

Dr. Günther Enderlein defines this subgenus as having that part of the median nervure beyond the external submedian cell obsolete and the cell open behind; the discoidal cell almost as large as the cubital and always touching the submedian cell; stigma long and narrow. Type: *H. macrurus* Schlett.

This group, or subgenus, appears to be confined to South America, being at present known chiefly from Brazil, with a few



from Colombia, Peru, and Chili. It seems probable that this is not the true distribution, or rather, that they are spread throughout the whole of the warm parts of the Southern Continent, their apparent absence being due to the absence of collectors.

The males are poorly represented, only 6 out of 17 species here recorded being known in that sex. Szépligeti briefly mentions *S. (H.) wiistenii*, ♂, stating merely "♂, tarsi four-jointed, metatarsus brown" (p. 534). The statement that the hind tarsi are four-jointed is repeated with respect to several other species, and seems inexplicable, seeing that he correctly gives others as five-jointed.

As a general rule, they are black insects with red head and nearly hyaline, or evenly infusate wings. The known exceptions are: *H. marginalis* Schlett. with black head, and *H. maculipennis* and *submaculatus* Westw. with centrally darker wings; the types of the two last are in the British Museum.

Roman works out this subgenus in (2), largely based on material collected by himself in the Amazon Region in 1914-15. He does not consider the difference in neurulation of the fore wing to be of sufficient value to justify the erection of a new genus—I prefer to call it a subgenus—and proposes to call it merely a group of the genus *Stephanus*. Three main reasons for this are advanced:—1st. That they differ from *Stephanus*, s. str., only in a single wing character, and that there is in the Stockholm Museum a transition form in which the external submedian cell is only slightly open. It is not unusual to find in *Stephanus*, s. str., that the apical transverse nervure bounding this cell does not actually join the median nervure, thus leaving the outer lower angle of the cell slightly open, but the median nervure, nevertheless, extends to the full length of the cell. 2nd. As far as is known, all the S. American *Stephanus*, s. str., are 25 mm. or more in length, *Hemistephanus* all less than 25 mm. I am unable to decide as to the value of this fact. 3rd. *Megischus texanus* Cress., originally described from a specimen with mutilated wings, is said to be represented in the Stockholm Museum by a topotype and to be a *Hemistephanus*, but differing in colour and sculpture from the S. American species, showing strong affinities to the N. American species of *Stephanus*, s. str. I should be not inclined to withdraw the subgenus on this evidence alone. There may be a mistake in identification, or the northern representatives of the group may have their special characters. For the present I place that species in *Stephanus*, s. str.

Practically nothing is known of the life-history of these insects. They are always found on or around dead or dying wood, and are certainly forest dwellers, parasitic on wood-boring larvæ. Roman (*l. c.*) suggests that their hosts are to be found among the Brenthidæ, their larvæ being elongate and apparently suitable for those of slender elongate insects like the Stephanidæ; also they are both found in all warm countries. Buprestidæ may also be considered, but Brenthidæ he thinks most probable.



## Table of Species.

♀.

- (18.) 1. Posterior margin of head produced collar-like.  
 (13.) 2. Petiole distinctly longer than rest of abdomen.  
 (4.) 3. Petiole twice as long as rest of abdomen; pronotum posteriorly rugose punctate; abdomen from second segment shining smooth; terebra about  $1\frac{1}{2}$  times as long as body. 1. *collarifer* Schlett.  
 (3.) 4. Petiole not more than half as long again as rest of abdomen.  
 (6.) 5. Head black; neck indistinctly transrugose, pronotum oblique, rugose behind ..... 2. *marginalis* Schlett.  
 (5.) 6. Head red.  
 (8.) 7. Neck transverse, hind coxæ smooth beneath ..... 3. *glabricoxis* Roman.  
 (7.) 8. Neck longer than broad; hind coxæ trans-striate beneath.  
 (10.) 9. Neck twice as long as broad; pronotum smooth, diffusely punctate behind only, median segment with punctures of varied size, interstices partly punctate-rugose... 4. *peruanus* Enderl.  
 (9.) 10. Neck not more than  $1\frac{1}{2}$  times as long as broad.  
 (12.) 11. Neck of pronotum laterally angulated; punctures on median segment uniform, interstices smooth ..... 5. *angulicollis* Roman.  
 (11.) 12. Neck of pronotum not laterally angulated; interstices on median segment alutaceous ..... [Cam. 6. *erythrocephalus*  
 (2.) 13. Petiole at most as long as rest of abdomen.  
 (15.) 14. Terebra scarcely longer than body; median segment centrally narrowly, laterally broadly impunctate ..... 7. *tener* Schlett.  
 (14.) 15. Terebra at least one-third longer than body.  
 (17.) 16. Petiole as long as rest of abdomen; terebra half as long again as body ..... 8. *wüstnei* Schlett.  
 (16.) 17. Petiole shorter than rest of abdomen; terebra one-third longer than body..... [Schlett. 9. *limpidipennis*  
 (1.) 18. Posterior margin bordered or not bordered, but not produced collar-like.  
 (26.) 19. Posterior margin of head bordered.  
 (21.) 20. Terebra twice as long as body; semiannular smooth and shining ..... 10. *macrurus* Schlett.  
 (20.) 21. Terebra not more than half as long again as body.  
 (23.) 22. Median segment confluent punctate.  
 (22 b.) 22 a. Scutellum smooth, with marginal punctures only. 27 mm. 11. *intermedius* Szépl.  
 (22 a.) 22 b. Scutellum closely punctate throughout. 13 mm. 11 a. *granulatus* Elliott.  
 (22.) 23. Median segment diffusely, not confluent punctate.  
 (25.) 24. Semiannular striate; metapleuræ coarsely alutaceous and punctate; hind coxæ closely rugose; wings hyaline. 12. *pehlkei* Enderl.  
 (24.) 25. Semiannular smooth; metapleuræ irregularly rugose; hind coxæ with sparse scale-like rugosities, wings subhyaline [Westw. centrally slightly darker..... 13. *submaculatus*  
 (19.) 26. Posterior margin of head simple, not bordered.  
 (28.) 27. Semiannular and petiole except basally smooth; wings subhyaline, centrally darker ..... [Westw. 14. *maculipennis*  
 (27.) 28. Semiannular more or less rugose; wings not centrally darker.  
 (30.) 29. Terebra more than half as long again as body; petiole as long as rest of abdomen ..... 15. *ruficeps* Cam.  
 (29.) 30. Terebra little or not longer than body.  
 (32.) 31. Terebra a little longer than body; petiole shorter than rest of abdomen; wings clear hyaline ..... 16. *vadosus* Schlett.  
 (31.) 32. Terebra only as long as body; petiole slightly shorter than rest of abdomen; wings infumate ..... 17. *cylindricus* Westw.

♂.

- (6.) 1. Posterior margin of head produced collar-like.  
 (3.) 2. Petiole shorter than rest of abdomen; collar short. 7. *tener* Schlett.  
 (2.) 3. Petiole longer than rest of abdomen.  
 (5.) 4. Petiole nearly twice as long as rest of abdomen ... 1. *collarifer* Schlett.  
 (4.) 5. Petiole a little longer than rest of abdomen; neck long and slender ..... 4. *peruanus* Enderl.  
 (1.) 6. Posterior margin of head simple, not bordered.  
 (8.) 7. Semiannular coarsely, obliquely rugose; 4th tergite finely longitudinally parallel striate; wings slightly infumate. 17. *cylindricus* Westw.  
 (7.) 8. Semiannular quite or nearly smooth.  
 (10.) 9. Wings clear hyaline; 4th tergite divergently longitudinally striate ..... 16. *vadosus* Schlett.  
 (9.) 10. Wings centrally darker ..... 14. *maculipennis* [Westw.]

## 1. COLLARIFER Schlett.

*Stephanus collarifer* Schlett., p. 141, ♀ ♂.

♀. Frons arcuate to oblique rugose; all five frontal tubercles prominent; occiput coarsely longitudinally to obliquely rugose; posterior margin of head reflexed and produced into a long, translucent collar. Basal flagellar joints normal. Neck with a strong transverse fold, behind which it is slightly transrugose; semiannular transrugose, laterally finely punctato-rugose. Mesonotum centrally smooth, with indistinct longitudinal row of punctures and two divergent, superficially punctate impressions, remainder transrugose and diffusely punctate. Scutellum smooth, with a few isolated but deep marginal punctures. Mesopleuræ finely alutaceous and shining above, sparsely punctate beneath; metapleuræ coarsely reticulate rugose, not separated from the median segment by any sulcus. Median segment with diffuse, shallow punctures, between which it is finely alutaceous; marginal sulci distinct and sometimes an indistinct central impression. Petiole transrugose, nearly twice as long as the smooth and shining remainder of abdomen, and almost longer than the hind coxæ, trochanters, and femora together. Terebra longer than body, its sheaths white-banded before apex. Hind legs with coxæ trans-striate between coarse, scale-like rugosities; femora polished smooth, bidentate; tibiæ compressed to beyond middle; tarsi three-jointed.

Black; head entirely, mandibles and antennæ basally ferruginous. Wings subhyaline; "neuration complete, excepting that part of the median nervure outside the submedian cell."

♂. Similar to the ♀, but head and thorax more finely sculptured, median segment closely cribrate punctate; hind tarsi five-jointed.

Length, ♀, 18 mm.; terebra 24 mm.; ♂, 12 mm.

Habitat: Brazil (Tefe on the Amazon and San Paulo Prov.); Surinam. Type in the Royal Nat. Hist. Museum, Berlin; co-type in coll. Wüstnei, in Sonderburg.

This species is distinguished from all others by the extremely elongate posterior margin of the head, and by the great comparative length of the petiole, which is twice as long as the rest of the abdomen.

## 2. MARGINALIS Schlett.

*Stephanus marginalis* Schlett., p. 133, ♀.

♀. Frons and occiput coarsely and irregularly rugose, a few arcuations immediately behind frontal tubercles. Posterior margin of head reflexed collar-like. Second flagellar joint three times as long as first; third as long as first and second together. Neck indistinctly finely rugose, especially centrally; semiannular finely obliquely rugose. Mesonotum centrally polished smooth, anteriorly and laterally rather coarsely transversely punctat rugose, the median line of punctures obsolete. Scutellum polished smooth, with a few very conspicuous punctures. Mesopleuræ almost smooth, with large, diffuse punctures; metapleuræ coarsely reticulate rugose, separated from the median segment by a polished smooth sulcus, which is broad in front, narrow behind. Median segment anteriorly smooth, centrally and posteriorly finely transrugose, coarser towards apex, with diffuse superficial punctures. Petiole basally distinctly, apically indistinctly transrugose, very little longer than rest of abdomen: second segment basally rugose, remainder of abdomen dull. Terebra scarcely longer than body, white-banded before apex. Hind legs with coxæ distinctly transrugose between widely placed scale-like rugosities; femora polished smooth, bidentate; tibiæ compressed to beyond middle.

Entirely black; wings slightly infumate. Length 25 mm.

Habitat: Bahia, Brazil. Type in Imp. Nat. Hist. Museum, Berlin.

This species strongly resembles *Stephanus furcatus* Lep. & Serv., *niger* Smith, and *sickmanni* Schlett., from all of which it may be distinguished—in addition to the neuration—by the reflexed posterior margin of the head and the elongate basal flagellar joints. The latter character, and the sculpture of the mesonotum will separate it from its nearest allies, *H. collarifer* Schlett. and *H. wüstneii* Schlett.

## 3. GLABRICOXIS Roman.

*Stephanus (Hemistephanus) glabricoxis* Roman (2), p. 9, ♀.

♀. Frons arcuate rugose, space between tubercles longitudinally rugose; vertex with 2–3 transcarinæ; occiput more longitudinally rugose; posterior margin of head collar-like, translucent. Scape as long as second flagellar joint; third joint rather longer than first and second together, fifth slightly shorter than fourth and as long as sixth. Neck transverse, apically deeply emarginate, transverse fold broad and deep; an oblique costa runs on each side of the fold, behind which the pronotum

is polished smooth; mesonotum anteriorly and laterally coarsely transrugose, posteriorly centrally smooth; impressed part of metapleuræ striate; median segment rugulose, especially laterally, the umbilical punctures do not extend to the sides; stigmal sulcus obsolete in front. Petiole slender, transrugose, longer than remaining segments; second basally transrugose, slightly aciculate beyond middle; third basally finely transreticulate, otherwise finely aciculate; fourth transverse, basal half transreticulate, apical half polished. Terebra one-third longer than body, its black apex more than half as broad as the subapical white band. Hind legs with coxæ polished smooth externally and beneath except towards apex, furnished with a few transverse piliferous granules, the usual close striation only visible above and inside; femora apically above and externally finely reticulate; tibiæ compressed to beyond middle; metatarsus about four times as long as broad. Fore wing not reaching apex of second segment.

Black; head except apices of mandibles, two basal antennal joints, and hind metatarsus red. Wings strongly infumate, stigma and nervures black, the former basally pale, radix and tegulæ black.

Length 18.5 mm.; terebra 24 mm.

Habitat: Cururuzinho, Rio Autaz, Brazil; 20.x.1914. One ♀ only.

Very similar to *H. angulicollis* Roman, differing especially in the sculpture of the short neck, the chiefly smooth coxæ and darker wings, as well as in minor details.

#### 4. PERUANUS Enderl.

*Hemistephanus peruanus* Enderlein (4), p. 302, ♀; Roman (2), p. 7, ♀ ♂.

♀ ♂. Head rather large; frons transrugose, straightly in front, arcuately behind. All five frontal tubercles well developed, the anterior one produced into a carina in front. Vertex and occiput arcuate rugose, posteriorly smooth, without central impression; posterior margin of head broad and translucent. Second flagellar joint about two and a half times as long as first; third about as long as first and second together. Pronotum elongate, polished smooth, with a few punctures on semiannular and a strong apical carina. Mesonotum anteriorly with a median row of punctures, on each side of which is a smooth space, bounded by two divergent rows of punctures, outside of which are four strong rugosities, dorsally smooth, with large diffuse punctures. Scutellum smooth. Mesopleuræ coarsely and diffusely granulate rugose, separated from the median segment by a wavy longitudinal carina. Median segment with large and small shallow punctures on a partly rugose punctate ground, a short longitudinal impression before spiracles, laterally indistinctly rugose, anterior lateral angles smooth polished. Petiole basally finely transrugose, apex broadly smooth, longer than remainder



of abdomen; second segment with extreme base finely rugose, then microscopically longitudinally aciculate; third to beyond middle and fourth basally finely shagreened and dull, remainder smooth. Terebra rather longer than body, white-banded before apex. Hind legs with coxæ finely transrugose throughout; femora bidentate, smooth.

Black; head and 3-4 basal antennal joints ferruginous, thorax basally dark red-brown. Tarsi densely gold pubescent beneath. Wings strongly infumate, nervures black-brown, stigma slender.

Length, ♀,  $19\frac{1}{2}$  mm.; abdomen  $13\frac{1}{2}$  mm.; petiole  $7\frac{1}{2}$  mm.; terebra  $21\frac{1}{2}$  mm.; fore wing  $11\frac{1}{2}$  mm. ♂,  $9\frac{1}{2}$ -14 mm.

Habitat: Prov. Chanchamayo (Rio Toro), Peru; Rio Autaz and Manaos, Brazil.

This species is best known from all others by the elongate, unsculptured pronotum. It resembles *Parastephanellus collarifer* Schlett., from which it may be distinguished by neuration of wings, sculpture of median segment and abdomen, and by the colour.

##### 5. *ANGULICOLLIS* Roman.

*Stephanus* (*Hemisteph.*) *angulicollis* Roman (2), p. 7, ♀.

♀. Frons arcuate rugose, space between the stout anterior tubercles longitudinally rugose, the posterior pair squamiform; vertex with 3-4 transcarinæ; occiput anteriorly more or less arcuately rugose, remainder smooth, centrally longitudinally aciculate, the rugose and smooth parts forming an obtuse angle with each other. Posterior margin of head produced into a translucent collar. Scape as long as second flagellar joint, third rather longer than first and second together, fifth as long as fourth and rather longer than sixth. Neck elongate, about one and a half times as long as broad; in front of the transverse fold is a broad sulcus, on each side of which is a strong raised costa running forwards and suddenly bent outwards, followed by others which become smaller in the direction of the fold; semiannular coarsely rugose before and below its polished posterior margin. Mesonotum with distinct central row of punctures, parapsidæ coarsely subtransversely rugose; impressed part of metapleuræ striate. Median segment with umbilicate punctures of about even size on a smooth ground, lateral impressions from spiracles to anterior margin. Abdomen more than twice as long as head and thorax, petiole slender, strongly trans-striate throughout, longer than the remaining segments together; extreme base of segment two transrugose, remainder polished and closely aciculate; third slightly longer than its apical breadth, basally finely transreticulate, rest aciculate, with broadly smooth apical margin; 3rd to 6th slightly apically emarginate; fourth not longer than its basal breadth, basal third transreticulate, centrally transaciculate, apically polished; remaining segments strongly transverse. Terebra about one-third longer than body, the black apex about



half as broad as the subapical white band. Hind legs with coxæ closely trans-striate, subobsoletely above, a few piliferous granules. Femora towards apex above and externally very finely reticulate; the tibiæ compressed to beyond middle; metatarsus five times longer than its maximum breadth. Fore wings not reaching apex of second segment.

Black; head except apices of mandibles, scape, first flagellar joint partly, and hind metatarsus obscurely red; palpi fuscous. Wings nearly hyaline; stigma black, basally narrowly pale; nervures and radix black, tegulæ pale, basally black.

Length 17.5 mm.; terebra 22 mm.

Habitat: Apipica, Rio Autaz, Brazil, 14.ix.1914. One ♀.

Apparently isolated by the peculiar structure of the neck, but near *H. peruanus* Enderl. in the elongate neck and small transverse fold.

#### 6. *ERYTHROCEPHALUS* Cam.

*Megischus erythrocephalus* Cameron (1), p. 421, ♀. *Stephanus e.* Schlett., p. 140, ♀.

♀. Frons transrugose; occiput longitudinally rugose, with faint central sulcus; posterior margin of head broadly bordered. Neck longitudinally sulcate, laterally obliquely carinate; semi-annular trans-striate, posterior margin narrowly smooth. Mesothorax trans-striate throughout; scutellum smooth, with three large marginal punctures on each side; meso- and meta-pleuræ and median segment alutaceous, with diffuse large punctures, the two latter separated by a sulcus. Petiole trans-striate, longer than rest of abdomen; second segment basally coarsely transrugose, thence and basal two-thirds of third discally longitudinally aciculate and dull, remaining segments smooth. Terebra slightly longer than body, sheaths white-banded before apex. Hind legs with coxæ coarsely trans-striate; femora smooth, bidentate; tibiæ constricted in basal third, apical third felted beneath.

Black; head red. Wings hyaline, stigma and nervures black.

Length 19 mm.; abdomen 13 mm.; petiole 7 mm.; terebra 20 mm.

Habitat: Buguba, Panama. Type in British Museum.

Closely allied to *H. collarifer* Schlett., but sufficiently distinguished by the less developed posterior margin of head and shorter terebra.

#### 7. *TENER* Schlett.

*Stephanus tener* Schlett., p. 142, ♀; Roman (2), p. 7, ♀ ♂.

♀. Frons finely arcuate rugose; occiput finely longitudinally to obliquely rugose, more transversely near posterior ocelli; the three anterior frontal tubercles very prominent; posterior margin of head produced into a short but distinct and translucent collar; cheeks scarcely as long as scape. Second flagellar

joint twice as long as first, third longer than first and second together. Neck elongate and very slender, posteriorly rugose, especially laterally; semiannular polished smooth, with a few fine punctures and oblique striations. Mesonotum laterally deeply punctato-rugose, with a central line of small but distinct punctures, on each side of which is a smooth space bounded by a row of broad punctures. Scutellum smooth, with a few conspicuous marginal punctures. Mesopleuræ rather smooth and shining above, dull beneath, with diffuse and shallow punctures; metapleuræ anteriorly finely and irregularly, posteriorly coarsely reticulate rugose, not separated by any sulcus from the median segment, which is punctate, except narrowly in the middle and broadly at the sides. Petiole transrugose, as long as remainder of abdomen; second segment smooth, basally rugose; third and fourth finely wavily transrugose, third centrally feebly longitudinally aciculate (in small individuals nearly smooth). Terebra as long as body, white-banded before apex. Hind legs with coxæ extremely finely transrugose between coarse, scale-like rugosities; femora polished smooth, bidentate; tibiæ compressed to beyond middle.

Black; head, scape, first flagellar joint, and mandibles basally ferruginous. Wings hyaline.

Length 9.3–14.5 mm. The type in the Hungarian National Museum at Budapest is 13 mm. long.

Habitat: type from Obidos on the Amazon, Brazil; Rio Autaz.

♂. Similar to ♀, but segment 4 subtransverse. Length 9–10.5 mm.

Habitat: Rio Autaz, Amazon District, Brazil; taken by Roman in 1914–15.

The elongate neck and shorter terebra will suffice to distinguish this species from *H. collarifer*, *limpidipennis*, and *wüstnei* Schlett., in all of which the neck is normal and the terebra longer than the body.

#### 8. WÜSTNEI Schlett.

*Stephanus wüstnei* Schlett., p. 149, ♀.

♀. Frons irregularly rugose; vertex transrugose; occiput rugose-punctate. Cheeks shorter than scape. Posterior margin of head produced into a very distinct collar. Basal flagellar joints normal. Neck with a few deep rugosities; semiannular polished smooth, with diffuse punctures. Mesonotum with a central row of punctures, on each side of which is a smooth space, laterally rather densely rugose-punctate. Scutellum smooth, with a few fine marginal punctures. Mesopleuræ almost smooth and slightly shining above, dull and rather coarsely and densely rugose-punctate beneath; metapleuræ reticulate rugose, more coarsely behind than in front, not separated from the median segment by any sulcus. Median segment densely

cribrate punctate, with a distinct crenulate sulcus on each side. Petiole very finely and indistinctly trans-striate, as long as the remaining segments; second segment basally striate, rest smooth and shining, with a few dull spots due to microscopic sculpture. Terebra half as long again as body, sheaths white-banded before apex. Hind legs with coxæ finely striated between coarse rugosities, distinctly transrugose beneath; femora polished smooth, bidentate; tibiæ compressed to beyond middle.

Black; head, mandibles basally, and scape ferruginous. Wings hyaline.

Length 12 mm.; terebra 18 mm.

Habitat: Massanary, on the Amazon, Brazil. Type in collection of Herr Wüstnei, after whom it is named.

Schletterer states that this species is deceptively like *H. limpidipennis*, but the sculpture of face is different, petiole and terebra longer, the former less distinctly sculptured and the median segment more densely punctate. From *H. marginalis* it may be distinguished by smaller size, shorter basal flagellar joints, shorter petiole, and shorter terebra.

Szépligetti, p. 533, states briefly of this species:—♂. Tarsi 4-jointed; metatarsus brown. ♀. Length 14 mm.; terebra 18 mm. Habitat: Fonteboa, on the Amazon, Brazil.

This error as to the ♂♂ having 4-jointed hind tarsi is repeated by him in other cases; they are always 5-jointed.

#### 9. LIMPIDIPENNIS Schlett.

*Stephanus limpidipennis* Schlett., p. 147, ♀.

♀. Frons rather coarsely and subarcuately rugose; vertex transrugose; occiput more coarsely punctato-rugose. Temples with a few punctures near eyes. Posterior margin of head produced into a long translucent collar. Cheeks decidedly shorter than scape. Basal flagellar joints normal. Neck of prothorax with two coarse transverse folds, between which it is deeply impressed and shining, behind them lightly punctato-rugose; semiannular rather densely, partly confluent punctate. Scutellum entirely smooth with a few marginal punctures. Mesonotum laterally rather coarsely and densely rugoso-punctate. Mesopleuræ smooth above, dull beneath, with large diffuse punctures; metapleuræ in front lightly and indistinctly, behind coarsely and deeply reticulate rugose, not separated from the median segment. Median segment shining smooth, with large diffuse punctures, centrally closer, marginal sulci distinct. Petiole trans-striate, basally irregularly rugose, distinctly shorter than remainder of abdomen, which is basally finely rugose, otherwise smooth with a few dull spots due to microscopic sculpture. Terebra evidently longer than body, white-banded before apex. Hind legs with coxæ finely trans-striate between very coarse rugosities; femora smooth, bidentate; tibiæ compressed to beyond middle.

Black; head, base of mandibles, and scape ferruginous. Wings extremely clear hyaline.

Length 14–15 mm.; terebra 19–20 mm.

Habitat: Massanary, Brazil. Type in Hungarian Nat. Museum, Budapest.

This species differs from *H. wüstnei* chiefly in the more arcuate rugose head, shorter and more coarsely sculptured petiole, and more diffusely punctate median segment. From *H. collarifer*, with which it agrees in size, colour, posterior margin of head, and length of terebra, it may be best known by the rugose-punctate occiput, shorter petiole, deeper sculpture of the semiannular, and by the very clear wings.

#### 10. *MACRURUS* Schlett.

*Stephanus macrurus* Schlett., p. 128, ♀.

♀. Frons rather finely arcuate rugose; occiput in front arcuately to transversely rugose. Posterior margin of head strongly bordered. Cheeks shorter than scape. Basal flagellar joints normal. Neck of prothorax apically finely transrugose, the remainder, together with the whole semiannular, smooth and shining. Mesonotum sparsely punctate, centrally smooth, with a longitudinal row of broad punctures, laterally finely transrugose. Scutellum polished smooth, diffusely and finely punctate. Mesopleuræ above finely alutaceous and shining, beneath dull, with large and partly confluent punctures; metapleuræ dull, finely and diffusely punctate, separated from median segment by an indistinct and finely rugose sulcus. Median segment with diffuse large punctures, interspersed with finer ones. Petiole transrugose, basally more coarsely, a little shorter than rest of abdomen, which is basally rugose, then shining, with a few dull spots. Terebra twice as long as body, sheaths white-banded before apex. Hind legs with coxæ shining, finely trans-striate; femora polished smooth, apically finely sculptured and subopaque, bidentate; tibiæ longer than femora, compressed not quite to middle.

Black; head ferruginous, mandibles red, apically brown; antennæ pitch-brown, apically ferruginous; neck of prothorax brown or rufous; hind tarsi rufescent. Wings hyaline.

Length 23–24 mm.

Habitat: Surinam. Type in Royal Natural History Museum, Berlin.

This species may be distinguished from *H. maculipennis* Westw. by the sculpture of petiole and hind coxæ, longer terebra, and hyaline wings. From *H. collarifer* Schlett. and *limpidipennis* Schlett., which it resembles in form and colour, it may at once be known by the much less prominent posterior margin of head and by the longer terebra.



## 11. INTERMEDIUS Szépl.

*Stephanus intermedius* Szépl., p. 533, ♀.

♀. Frons coarsely and indistinctly arcuately rugose; vertex arcuately, occiput transversely rugose; cheeks short, only half as long as scape; posterior margin of head sharply bordered. Basal flagellar joints normal. Pronotum short, irregularly trans-striate, its posterior margin polished. Mesonotum coarsely and irregularly rugose; scutellum smooth, with coarse marginal punctures. Mesopleuræ in front finely punctate, a few coarse punctures behind and transrugose below; metapleuræ pubescent, with a few isolated punctures, separated by a deep smooth sulcus from the confluent punctate median segment. The petiole transrugose, rather shorter than rest of abdomen. Terebra rather longer than body, white-banded before apex. Hind legs with coxæ trans-striate; femora smooth, bidentate; tibiæ compressed in basal third.

Black; head, scape, and hind tarsi ferruginous. Wings infumate, light brown.

Length 27 mm.; terebra 30 mm.

Habitat: Tonantins, Brazil.

This species comes very close to *H. macrurus* Schlett., from which it may be distinguished by the confluent puncturation of the median segment, infumate wings, and much shorter terebra.

## 11 a. GRANULATUS Elliott.

*Hemistephanus granulatus* Elliott (2), p. 130, ♀.

♀. Head, excepting the smooth temples, granulate rugose, vertex and occiput more finely; posterior margin of head bordered; anterior tubercle prominent; three very conspicuous carinæ between the posterior ocelli. Basal flagellar joints normal. Pronotum rather short, trans-striate, with smooth posterior margin; mesonotum centrally trans-striate, laterally punctate; scutellum closely punctate throughout, marginal punctures deep. Mesopleuræ finely and closely punctate; metapleuræ coarsely punctate, separated by a crenulate sulcus from the median segment, which is confluent, almost granulate punctate. Petiole trans-striate, slightly shorter than rest of abdomen; base of second segment trans-striate, remainder smooth, feebly shining. Terebra very nearly as long as body, rufescent. Hind legs with coxæ trans-striate; femora smooth, bidentate; tibiæ compressed to middle.

Rufescent; all metatarsi flavous to white. Wings infumate.

Length 13 mm.; abdomen  $7\frac{1}{2}$  mm.; petiole  $3\frac{1}{2}$  mm.; terebra  $13\frac{1}{2}$  mm.

Habitat: Swan River, West Australia.

The closely punctate scutellum and general granulate sculpture will distinguish this species.

If the label "Swan River" is correct, this is the first, and  
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up to the present, the only species of this subgenus known from the Australian Region. The large size of the discoidal cell places it here, but all other known examples come from South America.

12. *PEHLKEI* Enderl.

*Hemistephanus pehlkei* Enderl. (4), p. 304; Roman (2), pp. 10 et 13, ♀.

♀. Frons closely, posteriorly arcuately rugose; space between tubercles transrugose in front, obliquely behind. Vertex strongly arcuate rugose; occiput in front arcuate rugose, becoming finer and straighter behind, with a broad, indistinct median impression; posterior margin of head finely bordered. Second flagellar joint normal, third longer than first and second together. Neck rather short, with four transverse carinæ; semiannular moderately transrugose, the narrow posterior border smooth, and with lateral very fine oblique striation. Mesonotum anteriorly irregularly punctate rugose, with a median line of confluent punctures, centrally smooth, laterally coarsely punctate. Scutellum polished smooth, laterally coarsely punctate. Mesopleuræ rugose reticulate and diffusely punctate; metapleuræ similarly, but more coarsely punctate, separated from median segment by an anteriorly obsolete carina. Median segment smooth, with microscopic reticulation and diffuse punctures which do not touch the middle or sides; marginal sulci wanting. Petiole trans-striate, apically more finely, shorter than rest of abdomen. Second segment basally rugose, towards apex longitudinally aciculate; third to fifth basally granulate aciculate; fourth apically longitudinally aciculate, remainder very finely aciculate. Terebra one-third longer than body, sheaths black, a subapical white band as broad as the black apex. Hind coxæ transrugose; hind femora smooth, bidentate.

Black; head except apices of mandibles and 3 or 4 basal antennal joints ferruginous; hind tarsi gold pubescent beneath. Wings clear hyaline; stigma black, nervures black-brown.

Length (type)  $20\frac{1}{2}$  mm.; abdomen  $14\frac{1}{2}$  mm.; petiole 6 mm. terebra 28 mm.; fore wing  $10\frac{1}{2}$  mm. (Enderlein). 15– $20\frac{1}{2}$  mm. (Roman).

Habitat: Rio Magdalena, Colombia (Pehlke); Rio Autaz and Curururuzino, Amazon District, Brazil (Roman).

Roman states that this species is specially distinguished by the extremely fine oblique striation on the semiannular and at the lower end of the pleural furrow, also by the divergent longitudinal striation on the fourth tergite. The finely bordered posterior margin of the head and the carina between metapleuræ and median segment are characteristic, also the whole sculpture of the abdomen.

## 13. SUBMACULATUS Westw.

*Megischus submaculatus* Westw. (4), p. 230. ♀. *Stephanus s.* Schlett., p. 126, ♀.

♀. Frons arcuatè rugose; occiput anteriorly arcuately, posteriorly transversely rugose. Posterior margin of head very finely bordered. Second flagellar joint one and a half times as long as first, third as long as first and second together. Neck very finely trans-striate; semiannular entirely smooth. Mesonotum very diffusely and finely punctate; scutellum smooth, with a few marginal punctures. Mesopleuræ shining smooth above, diffusely punctate below; metapleuræ irregularly rugose, separated by a narrow but distinct sulcus from the median segment, which is very diffusely punctate, apically irregularly transrugose. Petiole trans-striate, a little shorter than rest of abdomen, with two very distinct lateral tubercles before middle; remaining segments smooth, apex of abdomen dull. Terebra longer than body, sheaths white-banded before apex. Hind coxæ with diffuse scale-like rugosities; hind femora polished, bidentate; hind tibiæ compressed to middle.

Black; head and scape red. Wings subhyaline, scarcely darker centrally.

Length 18 mm.; terebra 33 mm.

Habitat: Para, Brazil. Type in British Museum.

Very similar to *maculipennis* Westw., but differs in the almost smooth neck of pronotum, more diffuse puncturation of mesonotum and median segment, trans-striate petiole with much larger tubercles, and the subhyaline wings, not darker centrally.

## 14. MACULIPENNIS Westw.

*Megischus maculipennis* Westw. (4), p. 229, ♂. *Stephanus m.* Schlett., p. 127, ♂; Szépl., p. 533, ♀ ♂.

♀ ♂. Frons and vertex arcuate rugose; occiput regularly, laterally irregularly transrugose. Posterior margin of head simple. Second flagellar joint one and a half times as long as first; third normal. Neck very coarsely, basally more finely transrugose; semiannular polished smooth. Mesonotum coarsely and diffusely, laterally more densely and partly confluent punctate, the median row of punctures and lateral divergent impressions very distinct. Scutellum smooth, with a few conspicuous marginal punctures. Mesopleuræ above shining smooth, below finely and diffusely punctate; metapleuræ coarsely and irregularly rugose, separated by a narrow but distinct sulcus from the median segment, which is coarsely and diffusely punctate, apically transrugose. Petiole smooth, basally finely trans-striate, with a small tubercle on each side before the middle, shorter than rest of abdomen, which is subnitidulous, apically dull. Hind coxæ with diffuse coarse rugosities, only near posterior margin densely transrugose; hind femora polished smooth, bidentate; hind tibiæ longer than femora and compressed to middle.

Black; head entirely, frons and hind legs centrally ferruginous; mandibles and antennæ basally rufescent. Wings subhyaline, centrally strongly infumate.

Length 25-33 mm.; terebra 35-50 mm.

Habitat: Para, Brazil. Type of ♀ in British Museum.

Szépligetti (*l. c.*) states:—"♀. Length 25-30 mm.; terebra 35-50 mm.; sheaths white-banded before apex; posterior margin of head sharp; petiole transrugose; hind tarsi 3-jointed; otherwise as ♂. Yurimaquas, Peru, and Prov. Piauchy, Brazil.

Text-figure 4.



*Hemistephanus maculipennis.*

"Var. 1. ♀. Hind tibiæ entirely black. La Merced, Brazil.

"Var. 2. ♀ ♂. Median segment transrugose, centrally punctate. Wings pale brown to hyaline, centrally dark marked. Only basal half of front legs more or less red. Petiole of ♀ rather lightly transrugose. Length 33 mm.; terebra 50 mm. Vilcanota, Peru."

In the type-form the smooth petiole, centrally dark wings, and sculpture of prothorax will distinguish this species from *submaculatus* Westw. and *macrurus* Schlett., both of which it resembles. The transrugose petiole of Szépligetti's specimens appears to be merely a variety.

#### 15. RUFICEPS Cam.

*Megischus ruficeps*, Cameron (1), p. 420, pl. 18, fig. 9, ♀. *Stephanus capitatus* Schlett., p. 151, ♀. *Hemistephanus ruficeps* Morley (1), p. 112, ♀.

"Niger, capite rufo; alis fere hyalinis, ♀ long. 19 mm.; terebra 25 mm. *Hab.* Panama, Volcan de Chirique, 2500-4000 feet." (Cameron.)

♀. Head coarsely rugose, vertex more finely; posterior margin of head simple. Antennæ very slender, about two-thirds of length of body, scape elongate; basal flagellar joints normal. Neck coarsely, semiannular more finely trans-striate. Scutellum smooth, with large and coarse marginal punctures. Mesopleuræ aciculate, rather dull; metapleuræ rugose and dull. Median segment nitidulous, with large and diffuse punctures. Petiole irregularly but closely trans-striate, as long as remainder of abdomen. Terebra half as long again as body. Hind legs with coxæ striolate, more strongly towards apex, inner side densely pilose; femora smooth, bidentate; tibiæ and tarsi covered with dense, shining, fulvous pubescence.

Black with red head. Wings subhyaline.

Length 19-21 mm.; terebra 25-35 mm.

Habitat: Panama (Cameron); Amazon (Bates). Type in British Museum.

The present species may be best separated from *cylindricus* Westw. by the much longer terebra and by the sculpture of the pro- and meso-thorax and of the hind coxæ. It also resembles *H. wüstneii* Schlett., from which it may be known by the simple posterior margin of the head, coarser puncturation of the scutellum, and by the greater size.

In 1861, Smith described a *Fænatopus ruficeps*, and subsequently withdrew his genus *Fænatopus* as synonymous with *Stephanus*. On these grounds Schletterer (*l.c.*) altered the specific name to *capitatus*. More recent investigation has resulted in the original genus *Stephanus* being divided into a number of subgenera, in each of which it appears permissible to repeat a specific name; hence I restore the original name *ruficeps* given by Cameron.

#### 16. *VADOSUS* Schlett.

*Stephanus vadosus* Schlett., p. 146, ♀; Roman (2), p. 11, ♀ ♂.

♀. Head irregularly rugose, frons finely, occiput more coarsely and transversely in front; posterior margin of head simple. Second flagellar joint barely twice as long as first; third longer than first and second together. Neck feebly trans-rugose, semiannular polished smooth above, obsoletely rugose below. Mesonotum with irregular to transverse superficial rugosity, central row of punctures distinct, lateral ones indistinct. Scutellum polished smooth, marginally punctate. Mesopleuræ shining above, dull beneath; metapleuræ irregularly rugose, not separated from median segment, which is smooth shining, very diffusely punctate, with distinct marginal sulci. Petiole very finely trans-striate, little shorter than rest of abdomen; second segment basally finely rugose, apical third longitudinally striate, fourth longitudinally divergently striate. Terebra longer than



body, white-banded before apex. Hind legs with coxæ finely trans-striate between coarse ridges; femora smooth, bidentate; tibiæ compressed about to middle.

Black; mandibles and antennæ basally and hind metatarsus ferruginous; anterior legs brown, with a tendency towards rufescent. Wings entirely hyaline.

Length 12-20 mm.; terebra 15-24 mm.

♂. Differs from ♀ in having 3rd abdominal segment usually distinctly elongate, 4th transverse or rarely quadrate. Length 8-11.5 mm.

Habitat: Brazil, Manaos, Rio Autaz. Type in National Museum, Budapest.

This species appears to be one of the most frequent in the Amazon region, yet, until 1914, it had been only once taken, and the ♂ was not known. It comes close to *H. cylindricus* Westw., from which it may be distinguished chiefly by the finer sculpture of pro- and meso-thorax, longer terebra, and entirely hyaline wings. From *H. limpidipennis* Schlett., *wüstnei* Schlett., and *tener* Schlett., all of which it resembles, it is at once separated by the simple posterior margin of the head.

#### 17. CYLINDRICUS Westw.

*Megischus cylindricus* Westw. (4), p. 230. *Stephanus cylindricus* Schlett., p. 144; Enderlein (4), p. 306, ♀; Roman (2), p. 10, ♀ ♂.

♀. Head entirely finely and moderately irregularly rugose, more transversely near posterior ocelli; three anterior frontal tubercles very prominent; posterior margin of head simple. Second flagellar joint fully one and a half times as long as first; third longer than first and second together. Neck coarsely rugose, anteriorly transversely, posteriorly more irregularly; semiannular smooth above, laterally posteriorly obliquely rugose. Mesonotum rather coarsely rugose-punctate, a small central smooth space with indistinct longitudinal row of punctures, the lateral ones more distinct. Scutellum polished, with diffuse marginal punctures. Mesopleuræ shining smooth above, dull and diffusely punctate beneath; metapleuræ finely and diffusely punctate in front, irregularly rugose behind. Median segment strongly shining, very finely and diffusely punctate, marginal sulci obsolete. Petiole basally irregularly rugose, remainder distinctly trans-striate, a little shorter than rest of abdomen, also slightly shorter than the hind coxæ, trochanters, and femora together; second segment basally subrugose, third basally transversely, apically longitudinally striate, rest smooth, with a few dull spots due to microscopic sculpture. Terebra as long as body, sheaths white-banded before apex. Hind legs with coxæ finely striate between coarse rugosities; femora smooth, bidentate; tibiæ compressed to middle.

Black; head entirely, mandibles and antennæ basally ferruginous, hind tarsi badius. Wings slightly infusate.

Length 13-15 mm.



♂. Differs from ♀ in the stouter petiole, third segment not, or scarcely longer than its basal width, fourth strongly transverse (subelongate in ♀), its extreme base longitudinally striate. Length 19–14.5 mm.

Habitat: Rio Autaz, Apipica, Cururuzinho, Brazil; Peru, Dept. Chanchamayo.

This species seems by no means plentiful. It resembles *H. vadosus* Schlett., from which it may be known by the coarser sculpture of pro- and meso-thorax, shorter terebra, and colour of head. The simple posterior margin of the head and longer third flagellar joint will separate it from *H. limpidipennis*, *tener*, and *wüstnei* Schlett.

#### NEOSTEPHANUS.

Kieffer (1), p. 4, gen. n.

Smith's genus *Fœnatopus* was defined as having the cubital and discoidal cells wanting, or only indicated by indistinct nervures.

Kieffer (*l.c.*) subdivided this genus, placing in a new subgenus, *Neostephanus*, those species in which the apical margin of the external submedian cell is marked by a transverse nervure, while retaining in *Fœnatopus* those in which this nervure is absent.

The species of the subgenus *Neostephanus* appear to be confined to Central and South Africa and Madagascar, to which latter island the type-species, *N. alluaudi* Kieff., belongs.

#### Table of Species.

- |                                                                                                                                                              |                              |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------|
| (2.) 1. Hind femora tridentate; frons irregularly rugose; vertex with four trans-carinæ .....                                                                | 1. <i>alluaudi</i> Kieff.    |
| (1.) 2. Hind femora bidentate.                                                                                                                               |                              |
| (4.) 3. Temples rugose and dull except shining raised space near eyes; pro- and meso-notum closely rugose .....                                              | 2. <i>insignis</i> Schlett.  |
| (3.) 4. Temples smooth and shining.                                                                                                                          |                              |
| (6.) 5. Head large and globose; frons arcuate punctate...                                                                                                    | 3. <i>globiceps</i> Enderl.  |
| (5.) 6. Head ordinary; frons not arcuate punctate.                                                                                                           |                              |
| (10.) 7. Frons rugose.                                                                                                                                       |                              |
| (9.) 8. Frons obliquely rugose; median segment diffusely punctate.                                                                                           | 4. <i>camerunus</i> Enderl.  |
| (8.) 9. Frons subarcuate rugose; median segment coarsely and partly confluent punctate .....                                                                 | 5. <i>crassipes</i> Bischoff |
| (7.) 10. Frons reticulate.                                                                                                                                   |                              |
| (12.) 11. Vertex with one transcarina; 2nd and 3rd flagellar joints equal; mesopleuræ smooth; black, with white-marked head and abdomen .....                | 6. <i>albomaculatus</i> Cam. |
| (11.) 12. Vertex bicarinate; 3rd flagellar joint as long as first and second together; mesopleuræ granulose and dull; red-brown, abdomen yellow-marked ..... | 7. <i>pentheri</i> Kieff.    |

#### 1. ALLUAUDI Kieff.

*Neostephanus alluaudi* Kieffer (1), p. 1, ♀.

♀. Face and frons irregularly rugose, becoming arcuate towards the frontal tubercles, the space between which is not

impressed; vertex with four transcarinæ; occiput finely and densely trans-striate. Posterior margin of head simple. Second flagellar joint about one and a half times as long as first; third as long as first and second together. Neck transcarinate, semi-annular finely and densely trans-striate, posterior margin smooth and shining. Mesonotum irregularly rugose, with three longitudinal impressions; scutellum shining smooth, with a few marginal punctures, the lobes separated by rows of broad punctures. Median segment finely shagreened, shining and diffusely punctate. Petiole finely trans-striate, longer than rest of abdomen. Terebra shorter than body, sheaths rufescent, apically black. Hind legs with coxæ as long as trochanters and femora together, strongly trans-rugose; femora very finely shagreened, tridentate; tibiæ constricted beyond the middle, covered internally with dense erect red pubescence; tarsi densely pubescent beneath, metatarsus a little longer than the following joints together.

Black; head except apices of mandibles, basal third of antennæ, the front coxæ and legs, inflated part of hind tibiæ and all tarsi red; apical third of antennæ and the intermediate legs brown. Wings subhyaline.

Length 15 mm.; abdomen 9 mm.; terebra 12 mm.

Habitat: Madagascar, south of the Bay of Antongil and St. Marie de Madagascar. Three specimens taken by M. Ch. Alluaud.

(? Gold Coast, N. Territories, Yahi. Dr. J. J. Simpson, xi. 1916).

It is unfortunate that the type of the genus is the only one yet known with tridentate hind femora.

## 2. *INSIGNIS* Schlett.

*Stephanus insignis* Schlett., p. 100, ♀.

♀. Head rather coarsely and irregularly rugose throughout. Temples subrugose and dull, except a raised smooth and shining space near the ocelli. Posterior margin of head simple. Cheeks longer than scape. Second flagellar joint twice as long as first; third shorter than first and second together. Neck rather coarsely irregularly to transversely rugose; semiannular coarsely irregularly rugose. Mesonotum rather coarsely and irregularly punctat-rugose. Central section of scutellum anteriorly dull; behind this a small smooth polished space, laterally diffusely punctate, lateral lobes rather coarsely and densely punctate. Mesopleuræ polished smooth above, laterally rugose with rather dense indistinct puncturation; metapleuræ coarsely and irregularly rugose, separated by a smooth shining sulcus from the median segment, which is somewhat densely punctate. Petiole as long as, or slightly longer than rest of abdomen, trans-striate, remainder of abdomen smooth and shining. Terebra scarcely as long as body, spicula red, the sheaths ferruginous, apically black. Hind legs with coxæ and femora much incrassate, former coarsely and irregularly rugose, more transversely towards apex; femora finely

rugose-punctate and dull, bidentate; tibiæ constricted to beyond middle.

Black, with a tendency towards red; cheeks pale marked, mandibles and antennæ basally and frontal tubercles rufescent, a curved red line round anterior ocellus and all legs more or less red. Wings entirely hyaline.

Length 14 mm.

Habitat: South Africa. Type in Nat. Hist. Mus., Berlin.

This species may be best known by the rugose and dull temples, the dense and irregular sculpture of pro- and meso-notum, dense puncturation of scutellum, and median segment and red sheaths of terebra.

### 3. GLOBICEPS Enderl.

*Stephanus globiceps* Enderl. (1), p. 200, ♀.

♀. Head large and globose, its longitudinal axis very elongate, temples and occiput very long and convex. Frons arcuate punctate; all five frontal tubercles distinct; vertex coarsely transrugose; occiput finely arcuate rugose, with distinct longitudinal impression; posterior margin of head sharply bordered. Basal flagellar joints normal. Neck elongate, smooth, laterally obliquely rugose; semiannular trans-striate, posterior margin smooth. Mesonotum strongly transrugose and punctate. Scutellum centrally polished, laterally strongly punctate. Mesopleuræ pubescent, smooth, apical half diffusely punctate; metapleuræ alutaceous and dull in front, coarsely punctate behind, separated from median segment by a row of punctures. Median segment punctate, apically more densely. Abdomen wanting in the unique specimen. Hind coxæ finely trans-striate, their femora elongate, tarsi three-jointed.

Black; head ferruginous yellow; apex of mandibles and a transverse band between eyes black; five basal antennal joints, anterior legs, apices of hind femora with their tibiæ and tarsi ferruginous. Wings hyaline, very faintly infusate; stigma and nervures dark brown.

Length circa 14 mm.; the proportions of the remaining parts being about as in *N. insignis* Schlett.

Habitat: Johann Albrechtshöhe, N. Cameroons. March 1896; L. Conradt.

The shape, sculpture, and colour of head appear distinctive.

### 4. CAMERUNUS Enderl.

*Neostephanus camerunus* Enderl. (4), p. 299, ♀ ♂.

♀ ♂. Head medium; frons coarsely obliquely rugose, more transversely in front, almost circularly between the tubercles; vertex strongly, occiput less strongly arcuate rugose, with distinct posterior median impression. Posterior margin of head bordered. Basal flagellar joints normal. Neck short, coarsely obliquely rugose; semiannular smooth, posterior margin polished. Meso-

notum apically punctato-rugose, dorsally alutaceous between deep but diffuse punctures; scutellum polished smooth, laterally diffusely punctate, a row of about 10 subquadrate punctures on each side between it and the dorsum. Mesopleuræ with small and diffuse punctures and microscopic shagreening; metapleuræ widely reticulate, smooth above, separated from median segment by a carina, which passes into a row of punctures above in front. Median segment with diffuse, sharply-defined punctures, anterior lateral angles nearly smooth, apex rugose-punctate round the insertion of petiole. Petiole slender, finely trans-aciculate, extreme apex polished, longer than rest of abdomen in ♂, shorter in ♀; second segment basally rugose, remainder smooth. Terebra in ♀ twice as long as body, ferruginous brown, sheaths brown, broadly white-banded before apex. Hind coxæ rather slender, finely reticulate outside, trans-aciculate inside; femora bidentate. Radius in fore wing sharply geniculate and extending nearly to margin of wing.

Black; head—except mandibles apically, vertex, and space between frontal tubercles,—five basal antennal joints, all trochanters, tibiæ and tarsi, apices of hind femora, petiole laterally, apical segment dorsally only in ♀, entirely in ♂, and the male genitalia ferruginous; anterior femora brown. Wings hyaline, apically slightly infuscate; stigma and nervures brown.

Length, ♀, 18½ mm.; abdomen 13 mm.; petiole 5¾ mm.; fore wing 11 mm.; terebra 37 mm. ♂, 13 mm.; abdomen 8 mm.; petiole 5 mm.; fore wing 11 mm.

Habitat: Barombi, Cameroons. 1 ♀, 1 ♂; L. Conradt.

##### 5. CRASSIPES Bischoff.

*Neostephanus crassipes* Bischoff, p. 329, ♀.

♀. Frons subarcuate rugose; vertex transrugose; occiput punctate-rugose with central impression; posterior margin of head bordered. Antennæ normal. Prothorax smooth, laterally obliquely rugose; mesonotum irregularly punctate rugose; scutellum smooth, laterally strongly punctate. Mesopleuræ diffusely punctate; metapleuræ coriaceous in front, rather closely punctate behind, separated by a row of strong punctures from the median segment, which is coarsely, densely, and partly confluent punctate. (Details of petiole wanting.) Terebra much longer than body, sheaths black, white-banded before apex.

Black to black-brown; face below anterior tubercles, temples, cheeks, occiput laterally, four basal antennal joints, second segment laterally, third basally and ventrally, last segment entirely, hind trochanters, apices of hind femora, all tibiæ and tarsi more or less yellow-brown.

Length 19 mm.; terebra 27 mm.

Habitat: Kasindi, north of Lake Albert Edward. Jan. 1908.

Details as to the sculpture etc. of abdomen and as to hind legs



are wanting in the original description, and the unique specimen of *N. globiceps* was without abdomen, while the only details as to the hind legs are that the coxæ are trans-striate and the femora elongate.

Apparently very like *N. globiceps* Enderl., but frons less arcuately rugose, space between tubercles trans-striate, sculpture of occiput coarser and the impression less deep, puncturation of metapleuræ and median segment confluent.

#### 6. ALBOMACULATUS Cam.

*Fœnatopus albomaculatus* Cam. (7), p. 18, ♀.

♀. Frons closely and regularly reticulated; vertex dull, irregularly reticulate, with a transcarina behind tubercles; occiput irregularly closely striate, with an indistinct longitudinal impression. Second and third flagellar joints of equal length. Neck irregularly trans-striate, semiannular lightly reticulate; mesonotum basally reticulate, laterally obliquely striate; scutellum smooth and dull. Mesopleuræ smooth; metapleuræ finely reticulate. Median segment with round, clearly separated punctures, and microscopic sculpture. Petiole as long as thorax; terebra as long as body, sheaths black. Hind coxæ dull, coarsely aciculate, basally reticulate, apically striate; hind femora with a blunt, rounded basal tooth and two other long-pointed teeth.

Black; clypeus and a large spot on malar region whitish testaceous; mandibles basally and the carina on vertex rufescent; base and apex of petiole and a transverse spot at base of second segment white. Wings hyaline; stigma and nervures black.

Length 12 mm.; terebra 12 mm.

Habitat: Sebakwe, S. Rhodesia.

#### 7. PENTHERI Kieff.

*Neostephanus pentheri* Kieffer (2), p. 101; Morley (1), p. 111, ♂.

♂. Frons dull, reticulate; vertex with two transcarinæ; occiput finely rugose. Antennæ normal. Prothorax trans-rugose; mesonotum very short and transverse, finely shagreened, as is also the scutellum. Mesopleuræ closely granulose and dull; metapleuræ trans-striate and shining, separated by a carina from the median segment, which is as long as broad, reticulate and diffusely punctate. Petiole finely trans-striate, as long as remaining segments. Hind legs with coxæ transrugose; femora bidentate; tibiæ compressed in basal half; tarsi five-jointed, metatarsus longer than the four following joints.

Red-brown; mandibles black, antennæ basally pale, base and apex of petiole and a basal spot on each side of third segment yellow. Wings subhyaline; stigma black, basally white.

Length 10 mm.

Habitat: Zeruia, S. Africa. Taken by Dr. Penther in November.

The British Museum has a specimen taken in Angola in 1878 by J. J. Monteiro.



## FÆNATOPUS Smith.

This subgenus was erected in 1860 by Smith, to include all those species of *Stephanus* having reduced venation, but was restricted by Enderlein (Zool. Anz. xxviii. 1906) to those having only the basal cells complete, and a portion of the median nervure beyond the transverse nervure representing the upper boundary of the submedian cell. In *Diastephanus* this part of the median nervure is either entirely wanting or reduced to a mere stump. Although these subdivisions of the Stephanidæ may be said to be purely artificial, yet, since some of them appear to be confined to certain regions, and no transition forms are known, they seem to be founded on permanent differences, and are of the highest value in identifying the numerous species.

The number of teeth on the hind femora and the length of the petiole as compared with the rest of the abdomen, and, in the ♀, the length and colour of the terebra and its sheaths, are among the best characters for differentiation.

*Table of Species.*

♀.

- |        |                                                                                                                                                                                                     |                                 |
|--------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------|
| (25.)  | 1. Hind femora bidentate.                                                                                                                                                                           |                                 |
| (16.)  | 2. Petiole distinctly longer or shorter than rest of abdomen.                                                                                                                                       |                                 |
| (12.)  | 3. Petiole distinctly longer than rest of abdomen.                                                                                                                                                  |                                 |
| (5.)   | 4. Sheaths of terebra black; head arcuate striate ...                                                                                                                                               | 1. <i>ocellatus</i> Elliott.    |
| (4.)   | 5. Sheaths of terebra pale-banded before apex.                                                                                                                                                      |                                 |
| (7.)   | 6. Sheaths of terebra white-banded .....                                                                                                                                                            | 2. <i>indicus</i> Westw.        |
| (6.)   | 7. Sheaths of terebra yellow-banded.                                                                                                                                                                |                                 |
| (9.)   | 8. Terebra only as long as body .....                                                                                                                                                               | 3. <i>sumbanus</i> Enderl.      |
| (8.)   | 9. Terebra much longer than body.                                                                                                                                                                   |                                 |
| (11.)  | 10. Mesopleuræ closely punctate; 2nd segment basally smooth and shining .....                                                                                                                       | 4. <i>formosanus</i> Enderl.    |
| (10.)  | 11. Mesopleuræ very diffusely punctate; 2nd segment basally granulate and dull .....                                                                                                                | 5. <i>sulcaticollis</i> Enderl. |
| (3.)   | 12. Petiole distinctly shorter than rest of abdomen.                                                                                                                                                |                                 |
| (14.)  | 13. Terebral sheaths ferruginous, broadly yellow-banded, apex black. Head pale marked; middle tibiæ and hind metatarsus white .....                                                                 | 6. <i>annulitarsis</i> Enderl.  |
| (13.)  | 14. Terebral sheaths not yellow-banded; vertex transrugose.                                                                                                                                         |                                 |
| (15.)  | 14a. Sheaths ferruginous, apex black; mesonotum irregularly coarsely rugose; scutellum smooth and shining; metapleuræ and median segment alutaceous, separated by a carina. [Schultz.               |                                 |
|        |                                                                                                                                                                                                     | 7. <i>fernandopoensis</i>       |
| (14a.) | 15. Sheaths brown, apex black; mesonotum and scutellum densely rugose-punctate, latter with central smooth space; metapleuræ and median segment densely superficially punctate, not separated ..... | 8. <i>schlettereri</i> Enderl.  |
| (2.)   | 16. Petiole about as long as abdomen.                                                                                                                                                               |                                 |
| (18.)  | 17. Pronotum very short, densely rugose-punctate; terebra shorter than body, sheaths yellow-brown .....                                                                                             | 9. <i>brevicollis</i> Enderl.   |
| (17.)  | 18. Pronotum not very short.                                                                                                                                                                        |                                 |
| (22.)  | 19. Pronotum normal.                                                                                                                                                                                |                                 |

- (21.) 20. Neck oblique rugose, semiannular rugose-punctate; mesopleuræ punctate; terebra as long as body, sheaths red-brown, apex black ..... 10. *conradti* Enderl.
- (20.) 21. Neck trans-striate, semiannular and mesopleuræ smooth and shining; terebra shorter than body, black, white-banded before apex ..... [Schlett. 11. *lacteipennis*
- (19.) 22. Pronotum very elongate.
- (24.) 23. Neck trans-striate, semiannular and mesopleuræ smooth. 12. *longicollis* Cam.
- (23.) 24. Pronotum transrugose throughout. Rufo-piceous, abdomen white-marked ..... [Semenov. 13. *turcomanorum*
- (1.) 25. Hind femora tridentate.
- (29.) 26. Neck of pronotum very elongate.
- (28.) 27. Neck of prothorax alutaceous; hind femoral teeth black. 14. *simpsoni* Kieff.
- (27.) 28. Neck of pronotum finely striate; middle and apical hind femoral teeth white ..... 15. *variidens* Elliott.
- (26.) 29. Neck of pronotum not elongate.
- (31.) 30. Neck of pronotum very short; petiole shorter than rest of abdomen; terebra as long as body ..... 16. *arcuatus* Kieff.
- (30.) 31. Pronotum of ordinary length.
- (35.) 32. Frons striate, but not arcuately.
- (34.) 33. Frons finely trans-striate, occiput alutaceous; petiole shorter than rest of abdomen; terebra shorter than body. 17. *natalicus* Westw.
- (33.) 34. Frons rugosely trans-striate, occiput smooth; petiole longer than rest of body; terebra  $1\frac{1}{2}$  times as long as body. 18. *longicauda* Elliott.
- (32.) 35. Frons arcuate rugose.
- (37.) 36. Frons sparsely, almost granulately rugose; pronotum strongly trans-striate; legs rufescent; basal and central femoral teeth white, the apical black ..... 19. *rugiceps* Elliott.
- (36.) 37. Frons moderately arcuate striate to rugose; vertex and occiput trans-striate.
- (41.) 38. Neck of prothorax smooth.
- (40.) 39. Pronotum entirely smooth; terebra shorter than body, black. 20. *piceicornis* Cam.
- (39.) 40. Rest of pronotum trans-striate; terebra half as long again as body, white-banded ..... 21. *iridipennis* Elliott.
- (38.) 41. Neck of pronotum striate or rugose.
- (43.) 42. Pronotum strongly transrugose; lateral lobes of scutellum closely punctate ..... 22. *punctatus* Elliott.
- (42.) 43. Neck of pronotum more or less coarsely obliquely striate, remainder alutaceous.
- (45.) 44. Metapleuræ and median segment confluent, coarsely and superficially punctate. Terebra as long as body, ferruginous. 23. *togoensis* Stadlm.
- (44.) 45. Metapleuræ and median segment separated by a line of punctures, diffusely punctate; terebra shorter than body, black ..... 24. *claripennis* Elliott.

♂.

- (6.) 1. Hind femora bidentate.
- (3.) 2. Scutellum depressed, coarsely punctate; petiole shorter than rest of abdomen; 2nd segment basally longitudinally striate. Black; head bright rufo-testaceous ... 25. *aratifrons* Enderl.
- (2.) 3. Scutellum not depressed, only laterally punctate; petiole longer than rest of abdomen; 2nd segment basally smooth.

- (5.) 4. Frons and occiput finely transrugose; pronotum transrugose throughout; 2nd segment apically dull. Black; head yellow, vertex and occiput black ..... 4. *formosanus* Enderl.
- (4.) 5. Frons coriaceo-rugose, vertex and occiput transrugose; neck elongate, transrugose, semiannular smooth; 2nd segment basally smooth and shining. Black; head red, pale marked. 2. *indicus* Westw.
- (1.) 6. Hind femora tridentate.
- (10.) 7. Anterior frontal tubercles normal, larger than the posterior.
- (9.) 8. Frons transrugose, occiput alutaceous; pronotum trans-striate; petiole longer than rest of abdomen. Rufotestaceous, median segment apically black ..... 16. *natalicus* Westw.
- (8.) 9. Frons arcuate rugose, occiput finely transrugose and impressed; neck oblique striate; semiannular alutaceo-punctate; petiole as long as, or slightly shorter than rest of abdomen. Black; head, thorax, and legs ferruginous. 22. *togoensis* Stadlm.
- (7.) 10. Anterior frontal tubercles smaller than the posterior; vertex arcuate striate; mesonotum irregularly striate. Black; face, outer orbits, vertex, prothorax except central black line, meso- and meta-pleuræ, and anterior legs testaceous. 26. *flavicollis* Cam.

## 1. OCELLATUS Elliott.

*Fænatopus ocellatus* Elliott (2), p. 131, ♀.

♀. Head arcuate striate, occiput more finely; three strong carinæ between the posterior ocelli; posterior margin of head bordered; second flagellar joint one and a half times as long as first; third as long as first and second together. Neck elongate, trans-striate, remainder of pronotum subglabrous; mesonotum coarsely punctate; pro- and meso-pleuræ glabrous, metapleuræ and median segment cribrate punctate. Petiole trans-striate, longer than rest of abdomen; terebra shorter than body, black. Hind legs with coxæ trans-striate; femora smooth, bidentate; tibiæ compressed to middle.

Black; head and base of antennæ rufescent, ocellar region pale, and the ocelli deep, shining black; basal third of middle tibiæ and basal half of their metatarsi white. Wings hyaline, stigma yellow-brown.

Length 13 mm.; abdomen 8 mm.; petiole  $4\frac{1}{2}$  mm.; terebra 10 mm.

Habitat: Mount Matang, Sarawak. 18. i. 1914; G. E. Bryant.

The deep black ocelli are strikingly conspicuous against the pale rufescent background.

## 2. INDICUS Westw.

*Stephanus indicus* Westw. (2), p. 588; (3), p. 277; Schlett., p. 125, ♀ ♂. *Megischus indicus* Westw. (4). *Fænatopus ruficeps* Smith (2), p. 58, ♀. *Fænatopus indicus* Enderl. (3), p. 290, ♀, (4), p. 297; Morley (1), p. 36, ♀ ♂.

♀. Frons finely coriaceo-rugose; occiput finely trans-striate, with a shallow central longitudinal impression. Posterior margin of head bordered. Second flagellar joint one and a half times as

long as first; third nearly as long as first and second together. Neck elongate, very slender and finely transrugose above; semiannular shining smooth, laterally subrugose. Mesonotum lightly transrugose. Scutellum smooth and shining, with a few marginal punctures. Mesopleuræ polished smooth above, otherwise diffusely punctate; metapleuræ and median segment superficially cribrate punctate, not separated by any sulcus. Petiole slightly longer than rest of abdomen, rather shorter than hind coxæ, trochanters, and femora together, very finely trans-striate, remaining segments entirely smooth. Terebra slightly longer than body, sheaths white-banded before apex. Hind legs with coxæ slender, finely transrugose; femora dull, bidentate; tibiæ longer than femora, compressed to beyond middle.

Black; head red, frons and temples pale marked, anterior legs more or less brown, intermediate tibiæ and tarsi white-marked. Wings hyaline.

♂. Similar, but more coarsely sculptured, especially on median segment.

Length 11–14 mm.

Habitat: East India, Ceylon, Malabar, Philippines, Borneo, Sumbava, Celebes. Sumatra, a specimen measuring 19 mm. recorded by Dr. Dohrn.

Enderlein (*l. c.*) records specimens of this species, taken by Dr. Dohrn in Sumatra, having the impression on occiput more distinct, neck of pronotum more coarsely transrugose, semiannular transaculate in front, basal two-thirds of second abdominal segment polished smooth, remainder of abdomen dull, and hind femoral teeth black. Length 19–20.5; terebra 21–23 mm. This may prove to be a distinct species.

"Var. (?) ♀. Face finely alutaceo-rugose. Certainly a different species." Szépligetti, Termés. Füv. xxv. p. 531 (1902).

Habitat: Borneo.

### 3. SUMBANUS Enderl.

*Fenatopus indicus* var. *sumbana* Enderl. (4), p. 298; *F. sumbanus* Enderl. (3), p. 209, ♀.

♀. Frons finely coriaceo-rugose, occiput finely trans-striate; posterior margin of head slightly bordered. Second flagellar joint about one and a half times as long as first; third nearly as long as first and second together. Neck deeply transrugose, laterally finely and closely trans-striate, semiannular smooth above, without trace of sculpture, laterally finely and closely trans-striate, posterior angles strongly transrugose. Mesonotum irregularly to transversely rugose. Scutellum smooth, laterally finely aciculate with marginal punctures. Mesopleuræ rather smooth, diffusely punctate, with a central rugose and closely trans-striate space. Metapleuræ and median segment with large cribrate punctures. Petiole very finely and closely trans-striate, longer than rest of abdomen; second segment basally rugose,



centrally smooth, apically microscopically sculptured and dull. Terebra as long as body, sheaths black, with yellowish subapical band. Hind coxæ trans-striate; hind femora bidentate.

Black; head flavo-ferruginous, frons and vertex darker; basal half of second segment rufescent; anterior coxæ and legs, hind tibiæ and tarsi ferruginous, femoral teeth rufescent. Wings hyaline, stigma very long and narrowish, brown; nervures dark brown.

Length  $16\frac{1}{2}$  mm.; petiole 5.4 mm.; terebra  $16\frac{1}{2}$  mm.; fore wing 9 mm.

Habitat: Sumba, Malay Archipelago. 1 ♀; Grelak. Type at Stettin.

Differs from *F. indicus* in the sculpture of prothorax, shorter terebra, and colour. The femoral teeth are rufescent, whereas in *F. indicus* they are black (Enderlein), or white (Schlett.); the black apex of terebral sheaths is more than half as broad as the pale subapical band in *sumbanus*, but very much less in *indicus*.

#### 4. FORMOSANUS Enderl.

*Etenatopus formosanus* Enderl. (3), p. 207, ♀ ♂.

♀ ♂. Frons rather finely and irregularly transrugose, the ridges outwardly forked; occiput more finely rugose, with indistinct longitudinal median impression. Pronotum transrugose, more densely towards base, and intermixed with coarse punctures, lateral margins smooth, a broad posterior margin polished smooth and in front of it two roundish lateral spaces very finely and densely striate, having a velvety appearance, posterior angles strongly rugose. Scutellum polished smooth, laterally sparsely punctate. Mesopleuræ rather closely punctate, posterior margin very finely punctate and sparsely yellow pubescent. Petiole finely and densely trans-striate; second segment basally smooth and shining, apical half dull. Terebra in ♀ much longer than body, sheaths black, with a broad yellow band before apex. No details as to the hind legs are given.

Black; in ♀ frons black-brown, with three longitudinal rufo-testaceous lines, vertex and occiput black, remainder of head ferruginous yellow; in ♂ head light yellow, vertex and occiput black. Antennæ black, two basal joints yellow, third brown. Anterior legs from femora red-brown, tibiæ and tarsi in ♂ paler. Hind tarsi, sometimes also hind tibiæ, dark red-brown. Wings hyaline, stigma pale brown, nervures black-brown, apical nervure of median cell more or less pale.

Length, ♀, 12.4–17.75 mm.; petiole 4.5–7 mm.; terebra 16.5–24.5 mm.; fore wing 7.5–10.75 mm. ♂,  $10\frac{1}{2}$ – $16\frac{1}{2}$  mm.; petiole 4.6–6 mm.; fore wing 5.3–9 mm.

Habitat: Formosa, many localities, by H. Sauter, 1909–12; 18 ♀ ♀, 12 ♂ ♂. Co-types in Dahlen and Stettin Museums.

One large ♀, taken by H. Sauter in Hankau in 1912, has the nervure bounding the median cell pigmented throughout. Length



21.5 mm.; petiole 7 mm.; terebra 29 mm.; fore wing 12.6 mm. Enderlein states that the development and pigmentation of the nervure mentioned varies with the size of the individual, being shortest and palest in the smallest.

#### 5. *SULCATICOLLIS* Enderl.

*Fænatopus indicus* var. *sulcaticollis* Enderl. (4), p. 298. *F. sulcaticollis* Enderl. (3), p. 210, ♀.

♀. Frons finely coriaceo-rugose; occiput finely trans-striate, temples smooth polished; posterior margin of head slightly bordered. Second flagellar joint about one and a half times as long as first; third nearly as long as first and second together. Pronotum not rugose, but finely and densely trans-striate throughout, except the rugose posterior lateral angles and the smooth posterior margin. Mesonotum transrugose; scutellum smooth, with diffuse coarse marginal punctures. Mesopleuræ smooth, very diffusely punctate; metapleuræ and median segment cribrate punctate. Petiole finely and densely, but unusually superficially trans-striate, slightly longer than rest of abdomen; second segment with basal sixth granulate, apical half dull, central part smooth and shining. Terebra longer than body, sheaths black-brown with broad yellow subapical band. Hind coxæ more strongly trans-striate than the petiole; hind femora bidentate.

Black; head and three basal antennal joints ferruginous; apices of tergites 2-7 brownish; anterior coxæ dark ferruginous, anterior tarsi paler, hind tarsi black-brown. Wings hyaline, stigma very narrow, brown; nervures dark brown.

Length 18 mm.; petiole  $6\frac{1}{2}$  mm.; terebra 23 mm.; fore wing  $9\frac{1}{2}$  mm.

Habitat: Sumatra (Dr. Dohrn). Type in Stettin Museum.

From *F. indicus* Westw. and *F. sumbanus* Enderl. it differs in sculpture of pronotum and petiole as well as in colour, and from the latter also in the longer terebra.

#### 6. *ANNULITARSIS* Enderl.

*Fænatopus annulitarsis* Enderl. (3), p. 206, ♀.

♀. Frons, vertex, and occiput arcuate rugose. Pronotum strongly transrugose, laterally finely aciculate, posteriorly longitudinally striate; scutellum coarsely and densely punctate, posterior margin finely aciculate. Mesopleuræ smooth, closely punctate, posterior margin finely trans-striate, upper half yellow pubescent. Petiole finely and densely trans-striate; second segment smooth, basally rugose, remainder of abdomen dull. Terebra shorter than body, sheaths ferruginous, with indistinct yellow-brown band before the black apex. Basal half of hind coxæ transrugose; hind femora bidentate.

Black; face, cheeks, and temples ferruginous yellow; hind legs partly dark ferruginous; middle tibiæ and metatarsus

basally, hind metatarsus entirely whitish yellow. Teeth on hind femora black. Wings hyaline, stigma pale brown.

Length 9-14½ mm.; petiole 2.4-3.6 mm.; terebra 7.8-11.6 mm.; fore wing 5.7-7.8 mm.

Habitat: Taihorin, Kankau, Hoozan, Formosa. 1910-12; H. Sauter. Co-types in Dahlen and Stettin Museums.

#### 7. FERNANDOPOENSIS Schultz.

*Fœnatopus fernandopoensis* Schultz (1), p. 273, ♀.

♀. Frons finely and densely arcuate rugose, dull, with subobsolete longitudinal carina; vertex coarsely transrugose; occiput finely and irregularly rugose; cheeks finely and sparsely punctate. Posterior margin of head finely bordered. Basal flagellar joints normal. Pronotum alutaceo-rugose, extreme posterior margin polished smooth, laterally and apically diffusely punctate. Mesonotum irregularly and coarsely transrugose; scutellum centrally smooth and shining, laterally finely punctate and dull. Mesopleuræ with posterior larger half closely punctate. Metapleuræ and median segment finely alutaceo-punctate, latter discally diffusely and coarsely punctate, separated by a carina. Petiole finely and densely trans-striate, shorter than rest of abdomen. Terebra shorter than body, spicula and sheaths ferruginous, latter apically black.

Black; mandibles except apex, face and cheeks rufo-testaceous; ferruginous are five basal antennal joints, anterior legs (coxæ, trochanters, and femora nigrescent), hind coxæ apically, hind trochanters chiefly, basal half and apex of hind tibiæ and the tarsi, basal band on second and third abdominal segments, apex of third tergite obscurely and apex of last sternite. All the last tarsal joints and the claws black. Wings hyaline.

Length 9 mm.; terebra 7 mm.; fore wing 5 mm.

Habitat: Fernando Po. Type in coll. W. A. Schultz.

#### 8. SCHLETTERERI Enderl.

*Stephanus schlettereri* Enderl. (1), p. 201, ♀. *Fœnatopus schl.* (2), p. 474.

♀. Frons transrugose, with indistinct central carina; vertex coarsely transrugose; occiput irregularly and finely rugose-punctate; temples smooth, subrugose near the eyes. Posterior margin of head sharply bordered. Neck almost smooth; semi-annular polished smooth, laterally punctate. Mesonotum and scutellum densely rugose-punctate, latter with a small smooth central space. Metanotum not longitudinally striate. Mesopleuræ smooth, diffusely and superficially punctate; metapleuræ and median segment not separated, densely and superficially punctate. Petiole finely trans-striate, shorter than remainder of abdomen. Terebra rather shorter than body, sheaths yellow-brown, apically black. Hind coxæ finely trans-striate.

Black; mandibles except apex, basal half of antennæ, a streak on temples along eyes, the tegulæ, tibiæ and tarsi yellow. Wings colourless hyaline.

Length 10–11 mm.

Habitat: Johann Albrechtshöhe, N. Cameroons. L. Conradt; 1895–96.

Differs from *F. brevicollis* Enderl. in the formation of the propleuræ, reticulate transrugose face, longer and smoother pronotum, and shorter petiole.

#### 9. BREVICOLLIS Enderl.

*Stephanus brevicollis* Enderl. (1), p. 201, ♀. *Fœnatopus b.* (2), p. 474.

♀. Head densely granulate rugose; vertex transrugose; occiput densely punctate rugose. Posterior margin of head sharply bordered. Second flagellar joint a little longer than first; third and fourth as long as scape and about as long as first and second together. Pronotum short, densely punctate rugose; mesonotum and scutellum densely punctate, latter without any central smooth space; metanotum finely transrugose. Propleuræ separated from prothorax by a distinct acute-angled sulcus, produced into free-standing edges, which, seen laterally, appear like two sharp points. Mesopleuræ above smooth and shining, lower half punctate; metapleuræ and median segment separated only by a smoother streak, and both closely punctate. Petiole extremely finely trans-striate, as long as rest of abdomen. Terebra rather shorter than body; the spicula and sheaths, except black apex, yellow-brown. Hind coxæ finely trans-striate.

Black; mandibles except apex, three basal antennal joints, tegulæ, anterior tibiæ and all tarsi yellow-brown. Wings hyaline.

Length 7–10 mm.

Habitat: Bismarcksburg, Togo. L. Conradt; 1893.

This species appears to differ from all others in the peculiar formation of the propleuræ. From *F. schlettereri* Enderl. it further differs in the shorter prothorax and coarser sculpture of pro- and meso-notum.

#### 10. CONRADTI Enderl.

*Stephanus conradti* Enderl. (1), p. 202, ♀. *Fœnatopus c.* (2), p. 474.

♀. Frons very densely arcuately longitudinally rugose; vertex with three or four coarse ridges; occiput densely irregularly rugose, with subobsolete central channel. Temples subrugose near the eyes. Posterior margin of head slightly bordered. Basal flagellar joints normal, third slightly shorter than fourth and as long as scape. Neck obliquely rugose, remainder diffusely

punctate. Mesonotum indistinctly transrugose; scutellum nitidulous, with fine and diffuse small punctures. Metanotum relatively elongate, sharply longitudinally striate. Propleuræ separated from pronotum by a narrow sulcus; mesopleuræ rugose-punctate; metapleuræ rugose, apically trans-striate below, sparsely aciculate above. Median segment not very closely punctate, separated from the metapleuræ by a shining, curvate impression. Petiole finely striate, about as long as rest of abdomen. Terebra slightly shorter than body, sheaths red-brown, apically black. Hind coxæ finely trans-striate.

Black; mandibles basally, six basal antennal joints, anterior legs, apices of hind femora, basal half of hind tibiæ and hind tarsi red-brown or chestnut. Wings hyaline, nervures brown.

Length 15 mm.

Habitat: Bismarcksbuurg, Togo. L. Conradt; March 1893.

#### 11. LACTEIPENNIS Schlett.

*Stephanus lacteipennis* Schlett., p. 119, ♀.

♀. Frons rather finely and arcuately punctato-rugose; vertex arcuately rugose, occiput gradually more irregularly. Posterior margin of head simple. Basal flagellar joints normal. Neck finely but distinctly trans-striate; semiannular smooth and shining, apically and laterally finely trans-striate. Mesonotum rather coarsely transversely punctato-rugose. Scutellum with larger section smooth, lateral lobes diffusely punctate. Mesopleuræ smooth and shining, rugoso-punctate in front; metapleuræ and median segment very coarsely cribrate punctate, separated by an indistinct sulcus. Petiole finely trans-striate, about as long as remainder of abdomen and distinctly shorter than the hind coxæ, trochanters, and femora together; second segment basally finely rugose, rest of abdomen dull. Terebra slightly shorter than body, sheaths black, white-banded before apex. Hind legs with coxæ distinctly trans-striate; femora anteriorly shining smooth, posteriorly finely trans-striate and rather dull, bidentate; tibiæ not longer than femora, compressed to beyond middle.

Black; head, mandibles basally, and scape ferruginous; a pale streak from cheeks along eyes; anterior legs chestnut-brown, their joints pale marked. Wings milky white.

Length 22 mm.

Habitat: Borneo. Type in National Museum, Budapest.

The peculiar milky-white wings and short tibiæ are distinctive of this species.

#### 12. LONGICOLLIS Cam.

*Megiseleius longicollis* Cam. (3), p. 32, ♀.

♀. Frons coarsely and closely striate, obliquely above, transversely below; vertex and occiput closely obliquely striate, latter



with indistinct impression. (No details as to the proportions of the antennal joints are given, and these are broken off in the co-type in the British Museum.) Prothorax elongate, deeply incised at apex, the incision basally rounded; neck trans-striate, semiannular smooth. Mesonotum basally coarsely and irregularly reticulate, apically centrally impressed and laterally irregularly punctate. Scutellum smooth, laterally punctate. Mesopleuræ smooth, basally pilose; metapleuræ rugose. Median segment closely and coarsely punctate rugose. Petiole trans-striate, about as long as the smooth remainder of abdomen. Terebra longer than body, white-banded before apex. Hind coxæ closely but not strongly striate; hind femora bidentate.

Black; head pale rufous, orbits yellowish, three basal antennal joints, anterior legs, and base of second segment rufescent; prothorax brownish. Wings clear hyaline, stigma and nervures black.

Length 18–20 mm.; terebra 20–22 mm.

Habitat: Sarawak (Robert Shelford).

### 13. *TURCOMANORUM* Semenow.

*Stephanus turcomanorum* Semenow, p. 435; André, p. 488, ♀.

♀. Face and frons coarsely subtransversely rugose; vertex with two transearinae enclosing a falcate space; occiput trans-rugose; temples finely subrugose above, with a shining raised space near external margin of eyes, beneath which they are coriaceous; posterior margin of head simple but sharp. Third flagellar joint longer than second, but shorter than first and second together. Pronotum regularly transrugose, neck elongate. Mesonotum in front irregularly punctato-rugose, behind more feebly and subarcuately rugose. Mesopleuræ densely coriaceous-rugose; metapleuræ and median segment reticulate rugose, scarcely separated. Petiole finely and densely trans-striate, about as long as rest of abdomen. Terebra about as long as body, sheaths unicolorous nigro-piceous. Hind legs with coxæ regularly transrugose; femora finely coriaceous, dull, bidentate; tibiae constricted in basal two-thirds, and at the base of the clavate part irregularly and strongly impressed as if mutilated.

Rufopiceous; head, thorax, and legs chiefly rufescent; base and apex of petiole and two round spots on basal third of second segment white. Wings hyaline, stigma and nervures fuscous, former basally white.

Length 10 mm.

Habitat: Transcaspia; one ♀ taken near the military road to the station of Tedshe on the river of that name. Type in Mus. Zool. Acad. Caesar Scient. at Petropolsky.

This species is not unlike *F. indicus* Westw., but distinguished by the coarse sculpture of head and temples, and by the white-marked petiole and second segment.



14. *SIMPSONI* Kieff.*Fenatopus simpsoni* Kieffer (6), p. 233, ♀.

♀. Head subglobose, dull; frons coarsely and irregularly rugose, reticulate between tubercles, with median longitudinal carina; vertex transcarinate; occiput reticulate. First flagellar joint half as long as scape, second one and a half times as long as first; third and fourth of equal length and each twice as long as second. Pronotum elongate, dull, alutaceous, more strongly behind; mesonotum reticulate; propleuræ and sternum coriaceous; meso- and meta-pleuræ, scutellum, and median segment alutaceous, with large and diffuse punctures. Petiole densely trans-striate, as long as rest of abdomen. Terebra shorter than body, "composed of two red filaments, apically black and spatulate, without sheaths." The absence of the sheaths must have been due to accident. Hind coxæ closely trans-striate; hind femora tridentate, finely and indistinctly trans-striate; hind tibiæ only apically slightly inflated.

Black; mandibles except apices, cheeks, 4-5 basal antennal joints, a distal spot on each side of third segment, tibiæ and tarsi red; a spot on temples, one on vertex and the trochanters dull red; anterior femora and apical third of hind tibiæ brown-black; hind femoral teeth black; middle metatarsus whitish. Wings hyaline, stigma linear, yellowish hyaline.

Length 11 mm.; abdomen 6 mm.; petiole 3 mm.; terebra 10 mm.

Habitat: Ilon, South Nigeria; 13.iii.1910; J. J. Simpson, Entom. Research Committee.

15. *VARIIDENS* Elliott (4), p. 257, ♀.*Fenatopus variidens* Elliot (4), p. 257, ♀.

♀. Frons and ocellar space very finely striate; vertex and occiput transversely, almost arcuately striate; posterior margin of head strongly bordered. Cheeks slightly shorter than scape. Second flagellar joint one and a half times as long as first; third nearly as long as first and second together. Prothorax finely trans-striate, neck elongate, apically above deeply incised. Mesonotum irregularly rugose-punctate, central row of punctures distinct; scutellum centrally smooth, lateral lobes punctate. Mesopleuræ smooth; metapleuræ and median segment cribrate and confluent. Petiole finely trans-striate, slightly shorter than rest of abdomen. Terebra longer than body, with a 3 mm. broad white band before the 1 mm. broad black apex. Hind coxæ trans-striate; femora smooth, tridentate; tibiæ slightly longer than femora, compressed almost throughout.

Black; head ferruginous, frons darkest, inner orbits and anterior frontal tubercles paler; vertex, including ocellar space and occiput, black. Front tibiæ and tarsi rufescent; base of intermediate femora, their tibiæ externally and apical tarsal joints rufescent, metatarsus white; hind legs entirely black,

except the middle and apical femoral teeth, which are white. Wings iridescent hyaline, nervures pale brown, stigma centrally translucent.

Length 16 mm.; abdomen  $9\frac{1}{2}$  mm.; petiole  $4\frac{1}{2}$  mm.; terebra 18 mm.

Habitat: Paleboehan, Ratoe. M. E. Walsh (*ex* Frisby); 22nd February, 1916. Type in coll. Claude Morley.

The colour of the femoral teeth is distinctive. In *H. rugiceps* Elliott the basal tooth is white, the apical black; in the present species this is reversed.

#### 16. ARCUATUS Kieff.

*Fænatopus arcuatus* Kieffer (4), p. 118, ♀.

♀. Head subglobose; frons irregularly rugose, almost reticulate; vertex transcarinate; occiput irregularly rugose, with longitudinal sulcus; temples centrally prominent; posterior margin of head bordered. Second flagellar joint about one and a half times as long as first; third as long as first and second together. Neck very short, thorax cribrate punctate above throughout; median lobe of scutellum centrally slightly shagreened. Mesopleuræ diffusely cribrate punctate. Petiole densely transaciculate, rather shorter than rest of abdomen. Terebra as long as body, sheaths brown, apically black. Hind legs with coxæ trans-striate; femora tridentate; tibiæ compressed rather beyond middle.

Dull black; head entirely red, or occiput black-brown; five basal antennal joints red; anterior femora brown; all tibiæ and tarsi pale brown or brownish white. Wings hyaline, stigma and nervures brown. The radius curvate, not angulate, emitted from apical third of stigma.

Length 10 mm.

Habitat: Cameroons. Type in National Entom. Museum, Berlin. (Conradt.)

#### 17. NATALICUS Westw.

*Stephanus natalicus* Westw. (5), p. 127, pl. xxiv. fig. 8; Schlett., p. 102, ♀ ♂. *Neostephanus natalicus* Enderl. (2), p. 474. *Fænatopus natalicus* Morley (1), p. 110, ♀ ♂

♀ ♂. Frons finely transrugose, vertex transcarinate; occiput alutaceous. Posterior margin of head simple. Second flagellar joint one and a half times as long as first; third nearly as long as first and second together. Prothorax trans-striate. Mesonotum diffusely punctate; scutellum smooth. Meso- and meta-pleuræ nearly smooth, former pubescent, latter confluent with median segment, which is superficially and diffusely punctate. Petiole shorter than rest of abdomen, transaciculate, remainder smooth and feebly shining. Terebra shorter than body, fulvous, apically black. Hind legs with coxæ apically transaciculate; femora tridentate; tibiæ constricted to beyond middle. Tarsi five-jointed in ♂, three-jointed in female.

Fulvo-testaceous; antennæ basally nearly white; apex of median segment discally black; central abdominal segments apically nigrescent. Wings fuscous or fulvo-hyaline, iridescent, stigma pale.

Length, ♀, 10 mm.; abdomen 6 mm.; petiole  $2\frac{1}{2}$  mm.; terebra 8 mm. ♂,  $7\frac{1}{2}$  mm.

Habitat: Port Natal, S. Africa. Type in Hope Museum, Oxford.

In the British Museum are an old pair from F. Smith's collection with label "Port Natal," and a female with a green label from the same locality; all three were probably taken by the Swedish collector, Gueinzus, about 1859.

This species bears a strong superficial resemblance to *Diastephanus alutaceus* Morley, but, in addition to the venation, it may be distinguished easily by the sculpture of vertex and pronotum, and by the tridentate hind femora.

#### 18. LONGICAUDA Elliott.

*Fœnatopus longicauda* Elliott (2), p. 30, ♀.

♀. Frons transrugose, vertex finely trans-striate, occiput smooth and shining; frontal tubercles short and blunt; three stout carinæ between the posterior ocelli. Posterior margin of head simple. Basal flagellar joints normal. Prothorax finely trans-striate; mesonotum cribrate punctate; mesopleuræ smooth, with a few large punctures in the middle; metapleuræ coarsely punctate above, smooth below, separated by a crenulate furrow from the cribrate punctate median segment. Petiole trans-striate, a little longer than rest of abdomen, which is smooth and shining. Terebra half as long again as body, with a sharply-defined subapical white band, 2 mm. wide and  $1\frac{1}{2}$  mm. at apex, black. Hind coxæ trans-striate, basally more coarsely; hind femora very finely alutaceous and rather shining, tridentate; hind tibiæ compressed to a little beyond middle.

Black; mandibles except apex and face pale testaceous; anterior legs rufescent, tibiæ paler; hind tarsi rufescent. Wings basally infusate, nervures black.

Length 15 mm.; abdomen 10 mm.; petiole  $5\frac{1}{2}$  mm.; terebra 22 mm.

Habitat: Nilgiri Hills, India, 3000 ft.; 14th April, 1888 Sir George Hampson. Type in British Museum.

Very like *F. iridipennis* Elliott, but easily known by the infusate wings and smooth occiput with simple margin.

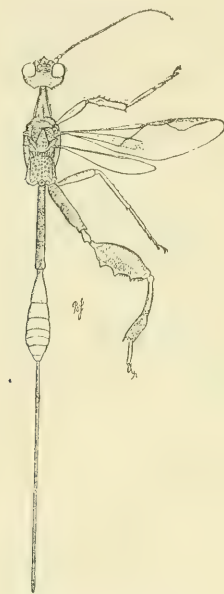
#### 19. RUGICEPS Elliott.

*Fœnatopus rugiceps* Elliott (2), p. 29, ♀.

♀. Frons granulate rugose, vertex and occiput subarcuate rugose. Frontal tubercles rather small and blunt, the space between them rugose; three carinæ between the posterior ocelli.

Posterior margin of head strongly bordered. Scape longer than cheeks. Second flagellar joint not quite half as long again as first; third about as long as first and second together. Prothorax strongly trans-striate, with rather broad smooth posterior margin; mesonotum coarsely punctate, apically smooth; propleuræ lightly punctate; mesopleuræ basally punctate, apically smooth; metapleuræ coarsely punctate, separated by a row of punctures from the median segment, which has large and diffuse punctures. Petiole trans-striate, as long as rest of abdomen, which is finely alutaceous. Terebra shorter than the body, basally rufescent, the colour gradually passing into an ill-defined subapical yellowish

Text-figure 5.

*Fœnatopus rugiceps.*

ring, extreme apex black. Hind coxæ coarsely transrugose, their femora tridentate, the basal tooth broad triangular, the central longer and more rounded, the apical narrow and very sharply pointed; hind tibiæ constricted in basal two-thirds.

Black; head rufo-testaceous, frons and vertex nigrescent, face and base of mandibles testaceous. Front legs rufo-testaceous, femora darker; middle legs lighter, with base of tibiæ and rather more than basal half of metatarsus white; hind legs rufescent, the basal and central femoral teeth white, the apical black, apex of tibiæ and the metatarsus except its apex white. Wings feebly infusate, nervures blackish.

Length 12 mm.; abdomen 7 mm.; petiole  $3\frac{1}{2}$  mm.; terebra 10 mm.

Habitat: South India. F. Smith coll. Type in British Museum.

The type bears a label with the MS. name "*F. ruficeps* Smith." A red head is very common in this subgenus and in no way distinctive. The rugosity of the head seems more characteristic. This species may be easily known by the colour of the femoral teeth, which appears to be a very constant character.

20. *PICEICORNIS* Cam.

*Fœnatopus piceicornis*, Cam. (10), p. 360, ♀.

♀. Frons subarcuately, vertex more distinctly arcuately rugose; occiput finely and closely trans-striate. Pronotum smooth; mesonotum in basal half strongly, irregularly reticulate, laterally coarsely punctate; scutellum smooth, laterally coarsely punctate. Median segment coarsely and diffusely punctate. Petiole finely trans-striate, as long as rest of abdomen. Terebra slightly shorter than body. Hind femora tridentate.

Black; outer orbits broadly yellow, mandibles apically rufo-testaceous, antennæ piceous, apically darker; anterior tibiæ and tarsi pale testaceous; hind trochanters, apex of tibiæ and the tarsi rufo-testaceous. Wings clear hyaline, stigma and nervures black.

Length 13 mm.; terebra 13 mm.

Habitat: Dima, West Africa (A. Koller). Type in Congo Museum, Tervueren.

The pale apex of mandibles is unusual, they are usually darker there.

21. *IRIDIPENNIS* Elliott.

*Fœnatopus iridipennis* Elliott (2), p. 30, ♀.

♀. Frons arcuate rugose, vertex and occiput finely and distinctly trans-striate; two short carinæ between the posterior ocelli; posterior margin of head bordered. Basal flagellar joints normal. Neck of pronotum smooth, rest trans-striate, with narrow smooth posterior margin. Mesothorax with large, well-separated punctures. Propleuræ finely striate; mesopleuræ finely alutaceous, metapleuræ and median segment cribrate punctate, separated by a carina. Petiole trans-striate, extreme apex smooth, as long as rest of abdomen; base of second segment trans-striate, remainder smooth. Terebra half as long again as body, white subapical band 2 mm. broad. Hind coxæ finely trans-striate, their femora tridentate; tibiæ constricted in basal two-thirds.

Black; head red, vertex black; the anterior tubercle has its front half red, the posterior half black. Anterior legs and hind tarsi rufescent, base of middle tibiæ and their metatarsus testa-



ceous. Wings hyaline, strongly iridescent throughout, nervures black.

Length 15 mm.; abdomen 10 mm.; petiole 5 mm.; terebra 22 mm.

Habitat: Dehra Dun, India. Nov. 1907; Lt.-Col. F. W. Thomson, I.M.S.

The sharply-defined red colour on the frons, including just the front half of the anterior tubercle, is unusual. May be distinguished from *F. longicauda* Elliott by the striate occiput, smooth neck of pronotum; and bordered posterior margin of head.

A male, tentatively placed with this female, differs in the finer sculpture of the head and striate metapleuræ. The base of the antennæ and the head are testaceous, with the vertex and part of occiput black. A very slender insect.

Length 11 mm.; abdomen 7 mm.; petiole 4 mm.

Habitat: Kangra Valley, 4000 ft. July 1889; Dudgeon.

## 22. PUNCTATUS Elliott.

*Fœnatopus punctatus* Elliott (2), p. 73, ♀.

♀. Frons arcuate rugose, vertex and occiput finely transrugose; posterior margin of head bordered; three carinæ between the posterior ocelli. Scape slightly longer than cheeks; basal flagellar joints normal. Pronotum strongly transrugose, with broad smooth posterior margin; mesonotum transrugose; central lobe of scutellum smooth, with a few large punctures, the lateral lobes closely punctate. Petiole finely trans-striate, shorter than rest of abdomen, which is smooth and shining. Terebra as long as body, white-banded. Hind coxæ transrugose; femora transrugose, tridentate; tibiæ compressed to middle.

Rufescent; a broad white band on each side under the eyes to base of mandibles. Wings hyaline, nervures rufescent.

Length  $13\frac{1}{2}$ – $16\frac{1}{2}$  mm.; abdomen  $8\frac{1}{2}$ –11 mm.; petiole 4–5 mm.; petiole  $13\frac{1}{2}$ – $16\frac{1}{2}$  mm.

Habitat: Burma. Two specimens in British Museum; the smaller with label "Birmah, F. Smith, coll."; the larger "Birmah" only.

The puncturation on the lateral lobes of scutellum is unusually dense.

## 23. TOGOENSIS Stadlm.

*Stephanus togoensis* Stadlm. (2), p. 80, ♂; Enderl. (1), p. 203, ♀ ♂. Var. *fasciatus* Enderl. l. c., ♀. *Diastephanus togoensis* Enderl. (2), p. 476; Morley (1), p. 113.

♂. Frons arcuate rugose; vertex with three or four coarse ridges; occiput rather more finely transrugose, with subobsolete central impression. Posterior margin of head slightly bordered. Second flagellar joint one and a half times as long as first; third

slightly shorter than first and second together. Neck of pronotum laterally obliquely rugose, remainder alutaceo-punctate; mesonotum coarsely punctate; scutellum smooth, with marginal punctures; metanotum longitudinally striate. Mesopleuræ diffusely punctate, upper margin polished; metapleuræ and median segment confluent, coarsely and superficially punctate. Petiole finely trans-striate, as long as, or slightly shorter than, remainder of abdomen. Hind coxæ trans-striate; hind femora tridentate.

Black; head, base of mandibles, five basal antennal joints, prothorax, tegulæ and legs, except hind coxæ and apex of hind femora, ferruginous. Wings hyaline, nervures dark brown.

Length 8-11 mm.

♀. Similar to ♂; terebra as long as body, spicula red-brown, sheaths ferruginous, apically black. Length 11 mm.

Habitat: Bismarcksburg, Togo. L. Conradt, 1893.

Var. *fasciatus* Enderl. More slender than the type-form; band across basal half of third segment rufescent; posterior femora basally dark.

Habitat: Johann Albrechtshöhe, North Cameroons. L. Conradt, 1895-96.

Dr. Enderlein (*l.c.*) places this species in his subgenus *Diastephanus*, but Stadelmann expressly states that the neurulation is exactly as in *F. indicus* Westw., and it is so closely similar to *F. conradti* that I incline to consider it merely a colour variety of that species. The different sculpture of scutellum and the absence of the slight smooth depression between metapleuræ and median segment appear to be the only differences. No mention of the femoral teeth is made in the description of *F. conradti*.

#### 24. CLARIPENNIS Elliott.

*Fœnatopus claripennis* Elliott (2), p. 81, ♀.

♀. Frons arcuate rugose, vertex subarcuate trans-striate, with distinct central longitudinal furrow, occiput more finely striate. Posterior margin of head bordered. A long, stout carina just in front of the posterior ocelli and two shorter ones between them. Scape as long as cheeks. Second flagellar joint one and a half times as long as first, third nearly as long as first and second together. Neck of pronotum coarsely, obliquely striate, the remainder alutaceous; mesonotum moderately punctate. Mesopleuræ alutaceous, basal half diffusely punctate; metapleuræ nearly smooth, with diffuse, large punctures, separated by a line of punctures from the median segment, which is alutaceous and diffusely punctate. Petiole trans-striate, its extreme apex smooth, as long as rest of abdomen. Terebra shorter than body, black. Hind legs with coxæ trans-striate, femora tridentate and very finely alutaceous, tibiæ constricted to middle.

Black; head rufescent, vertex darker; tegulæ, basal half of petiole and its apex broadly, and the second and third segments

basally red. Anterior legs rufescent, femora centrally and tibiæ partly darker; middle metatarsus yellowish; hind legs black, apex of femora, the tibiæ and tarsi rufescent. Wings very clear hyaline, apical half iridescent.

Length 15' mm.; abdomen 9 mm.; petiole  $4\frac{1}{2}$  mm.; terebra 13 mm.

Habitat: Nyassaland, Chiromo, Ruvo River. R. C. Wood, 1916. Type in British Museum.

The long red carina in front of the posterior ocelli and the sculpture of the prothorax sufficiently distinguish this species.

## 25. ARATIFRONS Enderl.

*Fœnatopus aratifrons* Enderl. (3), p. 207, ♂.

♂. Frons finely and densely, vertex and occiput more strongly transrugose. Pronotum with fine striation between coarser rugosities, laterally anteriorly alutaceo-granulate, posteriorly closely longitudinally striate. Scutellum depressed, coarsely punctate. Mesopleuræ sparsely punctate, posterior margin smooth, with fine trans-striation, upper third with sparse yellow hairs. Petiole densely trans-striate, second segment smooth, basally longitudinally striate, apically dull. Hind coxæ irregularly rugose, posterior fourth more regularly; hind femora bidentate.

Black; head bright rufo-testaceous; front coxæ and anterior legs ferruginous yellow; hind tarsi ferruginous, metatarsus pale yellow. Wings hyaline, stigma apically rounded, ochre-yellow; nervures brown.

Length 10.2 mm.; petiole  $2\frac{1}{2}$  mm.; fore wing 6 mm.

Habitat: Kankau, Formosa. H. Sauter. Type in Dahlen Museum.

## 26. FLAVICOLLIS Cam.

*Fœnatopus flavicollis* Cam. (10), p. 359, ♂.

♂. Anterior frontal tubercle smaller than the posterior, space between them obliquely striate; vertex arcuate striate. Mesonotum basally depressed and there bounded by a curved carina, and apical trans-sulcus, central part bounded by shallow oblique sulci and irregularly striate. Scutellum smooth, with irregular marginal punctures. Metanotum (median segment) diffusely punctate. Petiole dull and closely striate. Hind coxæ closely striate; hind femora tridentate.

Black; face, clypeus, outer orbits chiefly, scape, 3-4 basal flagellar joints, prothorax except central black line, meso- and meta-pleuræ, and anterior legs testaceous; vertex, base, and apex of hind tibiæ rufo-testaceous. Wings hyaline, stigma pale, nervures dark testaceous.

Length 8 mm.

Habitat: Dima, West Africa. A. Koller. Type in Congo Museum, Tervueren.

## DIASTEPHANUS Enderl.

Enderlein (2), p. 473.

This subgenus, as defined by Enderlein, has the lowest form of neururation, consisting of three basal cells and a widely open radial cell; the median nervure rarely extends beyond the transverse nervure, and then only as a short stump, whereas in *Pœnatopus* it extends to the full length of an outer submedial cell, or closely approximating that length. It occurs in the Ethiopian, Oriental, and Australian Regions, but has not yet been recorded from the Western Continent.

The species vary in size from 6 to 29 mm. in length, and the colour is, on the whole, brighter and more varied than in the other subfamilies; a white or flavous frons with rufescent lines is very common.

In preparing a table of species, I have experienced much difficulty in consequence of the want of details in some descriptions, in which, for instance, such important points as the sculpture of the head and the proportional length of the basal antennal joints are omitted. The colour of the terebral sheaths forms a good distinction in many cases, but these being broken in one species, renders it useless in that section. The colour of the terebra must always be understood to refer to the sheaths; the spicula is usually rufescent.

*Table of Species.*

♀.

- |       |     |                                                                                                                                                                                     |                               |
|-------|-----|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------|
| (20.) | 1.  | Hind femora tridentate.                                                                                                                                                             |                               |
| (11.) | 2.  | Petiole as long as rest of abdomen.                                                                                                                                                 |                               |
| (6.)  | 3.  | Hind femoral teeth white.                                                                                                                                                           |                               |
| (5.)  | 4.  | Femoral teeth milk-white; frons arcuate striate, mesonotum and median segment coriaceous and diffusely punctate; terebral sheaths red-brown, with broad subapical yellow band ..... | 1. <i>leucodon</i> Kieff.     |
| (4.)  | 5.  | Femoral teeth whitish; frons finely rugose, mesonotum coarsely irregularly rugose-punctate, median segment cribrate punctate, terebral sheaths black.....                           | 2. <i>pallescens</i> Schlett. |
| (3.)  | 6.  | Hind femoral teeth not all white.                                                                                                                                                   |                               |
| (8.)  | 7.  | Posterior margin of head produced into a collar; femoral teeth brown, median segment alutaceous .....                                                                               | 3. <i>fuscidens</i> Kieff.    |
| (7.)  | 8.  | Posterior margin of head bordered, but not collar-like.                                                                                                                             |                               |
| (10.) | 9.  | Sheaths of terebra black; neck short; hind femora punctate, the teeth black.....                                                                                                    | 4. <i>biróii</i> Szépl.       |
| (9.)  | 10. | Sheaths of terebra white-banded; neck elongate; hind femora trans-striate, central tooth white .....                                                                                | 5. <i>bilineatus</i> Elliott. |
| (2.)  | 11. | Petiole distinctly longer or shorter than rest of abdomen.                                                                                                                          |                               |
| (17.) | 12. | Petiole distinctly shorter than rest of abdomen.                                                                                                                                    |                               |
| (14.) | 13. | Body unusually slender, pronotum elongate and shining, frons densely striate .....                                                                                                  | 6. <i>gracilis</i> Kieff.     |
| (13.) | 14. | Body normal, prothorax not elongate, more or less dull.                                                                                                                             |                               |
| (16.) | 15. | Head finely reticulate, posterior margin simple...                                                                                                                                  | 7. <i>tertianus</i> Morley.   |
| (15.) | 16. | Head rugose, posterior margin bordered .....                                                                                                                                        | 8. <i>nova-guineensis</i>     |
| (12.) | 17. | Petiole distinctly longer than rest of abdomen.                                                                                                                                     | [Szépl.                       |

- (19.) 18. Metapleuræ and median segment finely reticulate-rugose; [Enderl.  
terebra shorter than body, sheaths red-yellow . 9. *flavomaculatus*
- (18.) 19. Metapleuræ and median segment irregularly coarsely rugose; [Schulthess.  
terebra as long as body, sheaths red-brown ... 10. *rothkirchi*
- (1.) 20. Hind femora bidentate.
- (38.) 21. Sheaths of terebra with subapical pale band.
- (23.) 22. Sheaths broadly yellow-banded; head small; second seg-  
ment finely punctate and dull; femoral teeth yellowish. [Enderl.  
11. *flavidentatus*
- (22.) 23. Terebral sheaths white-banded.
- (27.) 24. Hind femoral teeth white.
- (26.) 25. Anterior tubercle obsolete, frons transrugose, neck elongate,  
slender, median segment centrally basally smooth 12. *leucodontus* Schlett.
- (25.) 26. Anterior tubercle normal, frons arcuate striate, neck normal,  
median segment cribrate punctate throughout . 13. *elegans* Elliott.
- (24.) 27. Hind femoral teeth unicolorous with femora.
- (31.) 28. Frons rugose.
- (30.) 29. Frons with strong longitudinal carina, neck normal, meso-  
pleuræ and hind femora smooth ..... 14. *carinifrons* Enderl.
- (29.) 30. Frons not carinate, neck short and broad, mesopleuræ aciculate-  
punctate, hind femora aciculate ..... 15. *nigripes* Szépl.
- (28.) 31. Frons not rugose.
- (33.) 32. Head very small, frons alutaceous, neck granulate aciculate,  
metapleuræ and median segment with large hexagonal  
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- (32.) 33. Head normal.
- (35.) 34. Frons reticulate, neck transcarinate, metapleuræ finely acicu-  
late, petiole longer than rest of abdomen ..... 17. *frontilinea* Morley.
- (34.) 35. Frons trans-striate.
- (37.) 36. Frons arcuate striate, terebra shorter than body... 18. *trilineatus* Elliott.
- (36.) 37. Frons trans-striate, but not arcuately; terebra longer than  
body ..... 19. *chinensis* Elliott.
- (21.) 38. Sheaths of terebra unicolorous.
- (40.) 39. Body rufo-testaceous, femoral teeth white; terebra apically  
black ..... 20. *alutaceus* Morley.
- (39.) 40. Body chiefly black.
- (42.) 41. Petiole only half as long as rest of abdomen; head small; [Enderl.  
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- (41.) 42. Petiole much more than half as long as body.
- (46.) 43. Terebra about as long as body.
- (45.) 44. Frons finely trans-striate; first and second flagellar joints of  
equal length..... 22. *trilobatus* Elliott.
- (44.) 45. Frons transrugose: second flagellar joint one and a half times  
as long as first ..... 23. *dohrni* Enderl.
- (43.) 46. Terebra distinctly longer or shorter than body.
- (48.) 47. Terebra longer than body; frons arcuate rugose; two pro-  
minences on posterior half of hind femora strongly  
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- (47.) 48. Terebra shorter than body.
- (50.) 49. Terebra only half as long as body, Head small, frons arcuate  
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- (49.) 50. Terebra much more than half as long as body.
- (52.) 51. Anterior femoral teeth yellow, the posterior black. Head  
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- (51.) 52. Femoral teeth unicolorous.  
 (56.) 53. Femoral teeth white.  
 (55.) 54. Second flagellar joint one and a half times as long as first, third longer than first and second together; mesopleuræ smooth above; median segment strongly punctate [Enderl. throughout ..... 27. *maculifemur*  
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 (58.) 59. Second flagellar joint fully twice as long as first; petiole slightly shorter than rest of abdomen; 2nd segment smooth ..... 30. *celebensis* Szépl.  
 (57.) 60. Neck of prothorax normal.  
 (62.) 61. Frons irregularly rugose; abdomen from 2nd segment finely, densely punctate, dull ..... 31. *szépligetti* Enderl.  
 (61.) 62. Frons finely trans-striate, abdomen from 2nd segment smooth and polished ..... 32. *simillimus* Elliott.

## ♂.

- (6.) 1. Hind femora tridentate.  
 (5.) 2. Frons alutaceous, first and second flagellar joints of equal length; anterior legs yellow.  
 (4.) 3. Posterior margin of head bordered; neck finely rugose, semi-annular coarsely rugose; petiole about as long as rest of abdomen; femora finely and densely punctate. 33. *similis* Szépl.  
 (3.) 4. Posterior margin of head simple; pronotum nearly smooth; petiole distinctly longer than rest of abdomen; femora smooth and scarcely punctate ..... 34. *flaviceps* Elliott.  
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 (10.) 9. Petiole distinctly longer than rest of abdomen; pronotum and femoral teeth entirely black ..... 37. *fasciatus* Szépl.  
 (9.) 10. Petiole distinctly shorter than rest of abdomen.  
 (12.) 11. Anterior frontal tubercle obsolete; occiput very short; both femoral teeth white ..... 38. *flavonotatus* Elliott.  
 (11.) 12. Anterior frontal tubercle normal; occiput not short; posterior femoral tooth black ..... 26. *ruficollis* Enderl.

## 1. LEUCODON Kieff.

*Diastephanus leucodon* Kieff. (4), p. 116, ♀.

♀. Head subglobose; frons densely arcuate striate, vertex with three transcarinæ; occiput densely trans-striate, dull; posterior margin of head produced into a short collar. Basal flagellar joints normal. Neck elongate, densely striate; semi-annular coriaceous with smooth posterior margin. Mesonotum and median segment coriaceous, with large, diffuse and superficial

punctures. Scutellum centrally smooth and shining, marginal rows of punctures large and deep, lateral lobes dull. Pleuræ coarsely alutaceous. Petiole densely trans-striate, as long as rest of abdomen. Terebra nearly as long as body, spicula red, sheaths red-brown, with a clear yellow ring before the black apex. Hind legs with coxæ densely trans-striate; femora bidentate; tibiæ compressed in basal two-thirds.

Black; head except apices of mandibles, six basal antennal joints, prosternum, tegulæ, anterior legs except femora above, apex of hind coxæ, base and apex of hind femora, basal two-thirds of hind tibiæ, and apex of petiole clear red; space between anterior ocellus and posterior margin of head, anterior femora above and apical third of hind tibiæ brown; base of petiole, basal half of third tergite, a spot on each side of fourth and the hind tarsi yellowish white; hind femoral teeth milk-white. Wings hyaline, stigma and nervures subhyaline.

Length 10 mm.

Habitat: Cameroons. Type in National Entomological Museum, Berlin. (Conradt.)

Very like *D. fuscidens* Kieff., but differs chiefly in the sculpture of frons, pro- and meso-notum, and in the colour of the terebra and of the femoral teeth.

## 2. *PALLESCENS* Schlett.

*Stephanus pallescens* Schlett., p. 123, ♀. *Diastephanus pallescens* Enderl. (2), p. 475.

♀. Frons finely and more or less distinctly transrugose; occiput obconical, anteriorly rather coarsely trans-striate, posteriorly more irregularly rugose. Posterior margin of head bordered. Cheeks longer than scape. Second flagellar joint scarcely longer than first; third one and a half times as long as second. Neck elongate, very slender, finely trans-striate above; semiannular moderately finely rugoso-punctate, its posterior margin smooth. Mesonotum coarsely and irregularly punctat rugose. Scutellum finely punctate rugose. Mesopleuræ smooth and shining above, rather dull beneath, with a few indistinct punctures; metapleuræ and median segment somewhat coarsely cribrate-punctate, not separated. Petiole trans-striate, scarcely as long as rest of abdomen, which is feebly shining or dull. Terebra shorter than body, sheaths entirely black. Hind legs with coxæ transrugose; femora finely trans-striate and dull, tridentate; tibiæ longer than femora, compressed to beyond middle.

Black; face ferruginous, dull flavous towards eyes and on temples; mandibles and antennæ basally rufescent. Anterior legs chestnut-brown; teeth of hind femora whitish. Wings hyaline.

Length 11 mm.; terebra 8 mm.

Habitat: Philippines. Type in Town Museum at Hamburg.

This species resembles *D. leucodontus* Schlett., but the anterior tubercle is fully developed, second flagellar joint shorter, pro- and meso-notum more coarsely sculptured and hind femora tridentate. From *D. salomonis* Westw. it may be at once known by the conformation of the neck of prothorax and the tridentate hind femora.

### 3. FUSCIDENS Kieff.

*Diastephanus fuscidens* Kieff. (4), p. 118, ♀.

♀. Head subglobose; frons and vertex irregularly rugose, latter with three transcarinae in front; occiput trans-striate, dull; posterior margin of head produced into a collar. Second flagellar joint one and a half times as long as first; third longer than first and second together. Pronotum coriaceous, with polished posterior margin; mesonotum transrugose; scutellum centrally smooth and shining, marginal rows of punctures superficial. Pleurae alutaceous. Median segment alutaceous, with large, diffuse punctures. Petiole densely trans-striate, as long as remainder of abdomen. Terebra as long as body, spicula red, sheaths entirely black-brown. Hind legs with coxae trans-striate; femora tridentate; tibiae compressed to beyond middle.

Black; head except apices of mandibles, four basal antennal joints, basal half of third segment entirely, anterior legs, apex of hind coxae, hind femora entirely and hind tibiae basally red; hind tarsi testaceous; apical joint of all tarsi black; femoral teeth brown. Wings hyaline, stigma and nervures subhyaline.

Length 11 mm.

Habitat: Cameroons (Conradt). Type in National Entomological Museum, Berlin.

Very like *D. leucodon* Kieff., differing chiefly in the irregularly rugose frons, transrugose mesonotum, and in the colour of terebral sheaths and hind femoral teeth.

### 4. BIROI Szépl.

*Fœnatopus birói* Szépl., p. 530, ♀. *Diastephanus b.* Enderl. (2), p. 475.

♀. Frons irregularly, not transversely rugose; occiput short and rugose; posterior margin of head bordered. First and second flagellar joints of equal length. Neck short, subquadrate, anteriorly transversely, then irregularly rugose; semiannular coarsely rugose. Mesonotum coarsely rugose; scutellum centrally smooth, otherwise diffusely punctate. Mesopleurae with large, dense punctures, anteriorly dull. Median segment with large punctures, which are confluent and form rugosities on the apical half. Petiole finely striate, about as long as rest of abdomen. Terebra slightly shorter than body, sheaths black. Hind coxae finely trans-striate, their femora finely and densely punctate tridentate.

Black; cheeks and temples yellowish; mouth-parts, base of antennæ, anterior tibiæ mostly, and all tarsi yellow-red. Wings hyaline, stigma brown, tegulæ basally yellow.

Length 11 mm.

Habitat: Sinbang, New Guinea. Type in Hungarian National Museum.

##### 5. *BILINEATUS* Elliott.

*Diastephanus bilineatus* Elliott (2), p. 162, ♀.

♀. Head finely trans-striate; two carinæ between the posterior ocelli; all frontal tubercles distinct; posterior margin of head bordered. Second flagellar joint one and a half times as long as first; third longer than second, but shorter than first and second together. Neck of prothorax elongate, finely trans-striate, remainder smooth; mesonotum subglabrous, very diffusely punctate; pro- and meso-pleuræ very finely trans-striate; metapleuræ and median segment cribrate punctate, not separated. Petiole trans-striate, as long as rest of abdomen, which is smooth and shining. Terebra shorter than body, sheaths rufescent, with a subapical band  $\frac{3}{4}$  mm. broad, before the  $\frac{1}{2}$  mm. broad black apex. Hind coxæ and femora distinctly, their tibiæ less strongly trans-striate, the femora tridentate, tibiæ compressed to middle.

Black; head rufescent, mandibles except extreme apex, frons centrally broadly and orbits up to the level of the anterior tubercle flavous; point of abdomen below terebra white. Anterior knees pale rufescent, hind legs darker, with knees and metatarsi pale. Central femoral tooth white. Wings hyaline, iridescent; stigma and nervures brown.

Length 8-8½ mm.; abdomen 5 mm.; petiole 2½ mm.; terebra 7 mm.

Habitat: Pusa, Bihar; G. R. Dutt, 12. v. 09. Chapra, Bengal; Mackenzie.

The whole of the lower part of the head is white, excepting the more or less narrow rufescent lines separating the frons from the inner orbits. The sculpture of the head, the colour of the terebra and that of the femoral teeth will suffice to distinguish this species from all those with tridentate hind femora yet known. (May 1919.)

##### 6. *GRACILIS* Kieff.

*Diastephanus gracilis* Kieff. (5), p. 28, ♀.

♀. Body, especially abdomen, unusually slender. Frons dull and densely trans-striate, arcuately round anterior ocellus; vertex with five transcarinæ; occiput rugose, without central impression; posterior margin of head simple. Second flagellar joint little longer than first; third shorter than first and second



together. Pronotum elongate, shining, finely punctate, posterior margin rugose. Mesonotum coarsely transrugose; scutellum with central lobe finely punctate, with large marginal punctures, separated by rows of small punctures from the lateral lobes, which are alutaceous. Mesopleuræ finely alutaceous; metapleuræ reticulate rugose, the impressed part alutaceous. Median segment finely punctate with diffuse larger punctures, and with a broad crenulated sulcus on anterior margin. Petiole very slender, finely trans-striate, much shorter than rest of abdomen, which is coriaceous. Terebra little shorter than body, spicula red-brown, sheaths black. Hind legs with coxæ densely trans-rugose; femora finely alutaceous, tridentate; metatarsus partly and second tarsal joint entirely white pubescent beneath.

Black; head except apices of mandibles and occiput, four basal antennal joints, apex of petiole, basal half of third segment, apex of hind femora, the tibiæ and tarsi yellow or red; posterior coxa and femora brown. Wings whitish, stigma dark bordered, nervures pale yellow.

Length 13 mm.; terebra 12 mm.

Habitat: Mundame, Johann Albrechtshöhe, German East Africa. Conradt, 1906.

#### 7. TERTIANUS Morley.

*Diastephanus tertianus* Morley, p. 108, ♀.

♀. Head finely reticulate throughout; posterior tubercles and vertical carina small; cheeks much longer than scape; posterior margin of head simple. Second and third flagellar joints of equal length and about half as long again as first. Neck longitudinally sulcate, laterally obliquely carinate; semiannular microscopically sculptured and dull, without any smooth posterior margin. (Mesonotum destroyed by pin.) Scutellum dull and diffusely punctate. Mesosternum shining, finely alutaceous. Mesopleuræ alutaceous and sparsely punctate; metapleuræ finely transcarinate, confluent with median segment, which is finely reticulate and sparsely punctate. Petiole transaciculate, shorter than rest of abdomen, which is dull. Terebra rather shorter than body, sheaths black. Hind legs with the coxæ narrow, dull, and apically transaciculate; femora dull, tridentate; tibiæ longer than femora, constricted to middle.

Black; head, base of antennæ, prothorax, apex of petiole, base of second segment, basal two-thirds of third, and the legs red; base of hind femora and a mark inside apical third of hind tibiæ black. Wings hyaline; stigma lanceolate, centrally translucent; nervures brown.

Length 12 mm.; abdomen 7 mm.; petiole 3 mm.; terebra 10½ mm.

Habitat: Lesapi River, Mashonaland. Nov. 1897; Guy Marshall.



## 8. NOVA-GUINEENSIS Szépl.

*Ænatopus nova-guineensis* Szépl., p. 529, ♀. *Diastephanus nova-g.* Enderl. (2), p. 476.

♀. Frons finely rugose, laterally more transversely; vertex transrugose; occiput short and rugose, with distinct central apical sulcus; posterior margin of head bordered. First flagellar joint as long as second. Pro- and meso-notum coarsely rugose, neck short and broad. Scutellum only centrally smooth. Mesopleuræ dull, densely aciculate, with large, diffuse punctures. Median segment rather smooth, with large punctures. Petiole densely trans-striate, shorter than rest of abdomen. Terebra little shorter than body, sheaths black. Hind legs with coxæ coarsely transrugose; femora densely and finely alutaceo-punctate, tridentate.

Black; head except vertex, base of antennæ, anterior tibiæ and all tarsi yellow-red; anterior femora brown. Wings hyaline, nervures brown; stigma centrally yellow, tegulæ black.

Length 10 mm.

Habitat: Stephansort, New Guinea. Type in Hungarian National Museum.

Szépligetti states that in his *F. nova-guineensis*, *biró*i, *similis*, and *nigripes* the median nervure is prolonged outside the basal nervure. Enderlein (2) gives as the definition of his subgenus *Diastephanus*: "external submedian cell entirely wanting, there being at most a tiny remnant of the anterior bounding nervure," while, in *Ænatopus*, this nervure extends to the full extent of an external submedian cell. There might thus be some doubt as to the position of the above species; as, however, Enderlein places them in *Diastephanus*, I follow him.

## 9. FLAVOMACULATUS Enderl.

*Stephanus flavomaculatus* Enderl. (1), p. 205, ♀. *Diastephanus f.* (2), pp. 474-75.

♀. Frons indistinctly arcuate rugose; all frontal tubercles acuminate; vertex coarsely, occiput finely transrugose, without central impression. Posterior margin of head slightly bordered. Pronotum finely rugose, laterally deeply punctate just in front of the polished posterior margin; neck elongate. Mesonotum very coarsely transrugose; scutellum punctate, with central smooth space. Metanotum longitudinally striate. Metapleuræ and median segment finely reticulate rugose, separated by a fine raised line. Petiole rather finely trans-striate, longer than rest of abdomen. Terebra shorter than body, reddish-yellow, sheaths rust-yellow, apically black. Hind coxæ finely trans-striate; hind femora tridentate, teeth yellow.

Black; face, cheeks, five basal antennal joints, prosternum, anterior legs, and hind tibiæ ferruginous; median line and lateral margins of frons, base of petiole, apex of hind femora and spots

on segments 3-5, also apex of last segment yellow. Wings hyaline, nervures pale brown.

Length  $12\frac{1}{2}$  mm.

Habitat: Johann Albrechtshöhe, N. Cameroons. L. Conradt, 1896.

There appears to be a very remarkable similarity between the specimens of this group of Stephanidæ from Johann Albrechtshöhe, North Cameroons, and, since several are described from single specimens only, and none from any sufficient number, there may be doubts as to the distinctness of the species. The difficulty of deciding this matter is greatly increased by the fact that the descriptions vary in the amount of the details; the relative length of the basal antennal joints, and especially details as to the hind legs and femoral teeth, are often wanting. In addition to this, Dr. Enderlein (1) gives a table of the African species of *Stephanus*—as then known to him—in which he gives characters differing from those in the detailed descriptions. Thus: *terebellus*—median segment (*a*) not separated from metapleuræ, (*b*) separated by a raised carina; *togoensis*—scarcely or not at all separated; *flavomaculatus*—neck (*a*) obliquely striate throughout, (*b*) finely rugose; *brevipetiolatus*—face (*a*) irregularly reticulate, (*b*) finely arcuate rugose. While provisionally retaining these species, further information is required to settle their claims.

#### 10. *ROTHKIRCHI* Schulthess.

*Diastephanus rothkirchi* Schulthess, p. 283, ♀; Morley (1), p. 113, ♀.

♀. Frons irregularly and partly arcuately rugose; vertex with four transcarinae; occiput strongly transrugose, without longitudinal impression. Posterior margin of head sharply bordered. Scape as long as first and second flagellar joints together; second longer than first; third shorter than first and second together. Pronotum finely transrugose; semiannular centrally finely transrugose, laterally coarsely and irregularly punctate. Mesonotum coarsely rugoso-punctate; scutellum centrally smooth, with a few marginal punctures, lateral rows of punctures distinct, lateral lobes finely transrugose. Mesopleuræ finely rugose and diffusely punctate; metapleuræ confluent with median segment, and, like it, irregularly and coarsely rugoso-punctate, interstices and bottom of punctures very finely transrugose. (A few lines before this, the author states "median segment longer than mesonotum and scutellum, finely faceted, between the facets very finely transrugose.") Petiole finely transstriate, longer than rest of abdomen; second segment basally coarsely rugoso-punctate, remainder of abdomen smooth. Terebra as long as body, spicula red-brown, sheaths brown, paler before the black apex. Hind legs with coxæ and femora finely transrugose, latter tridentate; teeth in three groups, the central of one tooth only, largest of all; the basal and apical groups of two each, of which the inner is smallest; apex of tibiæ and inside of tarsi clothed with dense red-grey pubescence.

Black; head red except apices of mandibles and the occiput; 4-5 basal antennal joints, pronotum laterally and beneath, a basal band on third tergite, ventral surface of second sternite, all coxæ and legs red; petiole basally, knees and middle metatarsi basally white, hind coxæ and base of hind femora black. Wings hyaline, stigma elongate, narrow lanceolate, brownish; nervures dark brown.

Length 10 mm.; abdomen 6 mm.; petiole 3.5 mm.; wings 3.5 mm.; terebra 10.5 mm.

Habitat: Cameroons. Oberlieutenant v. Rothkirch, German Colonial Defence Force.

A specimen in the British Museum (M'Langa, Nyassaland, S. A. Neave, 2. i. 1914) differs from the above description only in having a more red-brown petiole and second segment black.

This species comes near *D. szepligetii* Enderl. and *D. gracilis* Kieff., but differs from both in size and sculpture. The number of minor denticulations between the larger hind femoral teeth appears to vary, but we do not possess sufficient details to decide whether this is an individual or specific difference.

#### 11. FLAVIDENTATUS Enderl.

*Diastephanus flavidentatus* Enderl. (3), p. 204, ♀.

♀. Head rather small, globose. Neck strongly transrugose, laterally more finely and closely, semiannular finely trans-striate, apically more closely, posterior margin laterally rugose. Mesopleuræ sparsely and coarsely punctate, posterior margin smooth, upper third finely transrugose and yellow pubescent. Petiole finely transrugose; second segment dull, finely punctate and basally indistinctly rugose. Terebra rather longer than body, sheaths with broad yellow band before apex. Hind femora bidentate; hind tibiæ and metatarsus yellow pubescent.

Black; face, cheeks, lateral borders of frons, and a median line yellow; antennæ brown, basally paler. Anterior legs pale ferruginous; a streak on outside of basal fourth of front tibiæ, basal fourth of middle tibiæ and basal half of middle metatarsus yellow. Hind legs black-brown, tarsi rufescent, femoral teeth yellowish. Wings hyaline; stigma pale yellow, nervures brown.

Length  $11\frac{1}{2}$ – $14\frac{1}{4}$  mm.; petiole 4.1–5.2 mm.; terebra  $13\frac{1}{2}$ –15 mm.; fore wing 7– $8\frac{1}{2}$  mm.

Habitat: Formosa, 1911; Kankau, 1912; Hoozan, 1910. H. Sauter. Co-types in German Ent. Museum at Dahlen and in Stettin Museum.

Enderlein (*l.c.*) states that the only other species in this subgenus having yellow femoral teeth are his *D. maculifemur* and *D. ruficollis*. The detailed descriptions state clearly that in *D. maculifemur* both teeth are white, and in *D. ruficollis* the anterior tooth is yellow, the posterior black. The present species differs from *D. ruficollis* in the sheaths of terebra being yellow-banded, hind tibiæ pubescent, and both femoral teeth yellow; from *D. maculifemur* in smaller head, longer terebra, and in the colour of terebral sheaths and femoral teeth.

12. *LEUCODONTUS* Schlett.

*Stephanus leucodontus* Schlett., p. 121, ♀. *Diastephanus l.* Enderl. (2), p. 475.

♀. Frons finely, transversely coriaceous-rugose; anterior frontal tubercle wanting (otherwise always present); occiput very short, finely trans-striate, more coarsely behind the ocelli. Posterior margin of head simple; cheeks longer than scape. Second flagellar joint one and a half times as long as first; third longer than first and second together. Neck elongate and slender, obsoletely trans-striate; semiannular subnitidulous, with a central longitudinal trans-striate fovea. Mesonotum finely and irregularly transrugoso-punctate. Scutellum entirely smooth. Mesopleuræ smooth and shining, with a few superficial punctures below; metapleuræ smooth and shining in front, rather coarsely reticulate-rugose behind. Median segment centrally and basally smooth, laterally with large punctures, which are more dense apically. Petiole very finely transrugose, as long as rest of abdomen, which is smooth and strongly nitidulous. The terebra broken off. Hind coxæ slender, trans-striate; hind femora entirely smooth, bidentate; hind tibiae compressed to beyond middle.

Black; frons rufo-testaceous, rest of head ferruginous; antennæ basally testaceous; pronotum and legs brown; teeth of hind femora white, and hind tarsi white-marked. Wings entirely hyaline.

Length 10 mm.

Habitat: Sarawak. Type in Royal Nat. Hist. Museum, Berlin.

The absence of the usually well-developed frontal anterior tubercle will distinguish this species from all others. It closely resembles *D. pallescens* Schlett. and *F. indicus* Westw. It may be distinguished from both by the short occiput, simple posterior margin of head, and by the sculpture of the hind femora; from *F. indicus* Westw. it further differs in the neurulation.

A specimen in the British Museum, from Singapore, has a white-banded terebra; length of body  $10\frac{1}{2}$  mm.; terebra 9 mm.

13. *ELEGANS* Elliott.

*Diastephanus elegans* Elliott (2), p. 31, ♀.

♀. Frons finely arcuate striate; vertex trans-striate; occiput nearly smooth. Space between the posterior ocelli trans-striate. Posterior margin of head bordered. Basal flagellar joints normal. Pronotum very finely trans-striate and rather shining, basal margin smooth; mesonotum almost smooth. Central lobe of scutellum finely punctate. Propleuræ finely striate; mesopleuræ smooth and shining; metapleuræ and median segment cribrate punctate, separated by a carina. Petiole extremely finely trans-striate, shorter than rest of abdomen, which is smooth and



shining. Terebra shorter than body, sheaths white-banded. Hind coxæ trans-striate, their femora bidentate; tibiæ compressed to middle.

Black; head rufo-testaceous, vertex slightly darker; three basal joints of antennæ, prosternum, tegulæ, and anterior legs rufo-testaceous, the femora rather darker, tarsi paler, middle metatarsus whitish; hind legs darker, with the metatarsus paler. Femoral teeth white.

Length  $6\frac{1}{2}$  mm.; abdomen  $3\frac{1}{2}$  mm.; petiole  $1\frac{1}{2}$  mm.; terebra 5 mm.

Habitat: Singapore. H. N. Ridley, 1900. Type in British Museum.

A delicate insect, distinguished by the space between the posterior ocelli being striate, instead of, as usual, carinate, and by the white femoral teeth.

#### 14. CARINIFRONS Enderl.

*Diastephanus carinifrons* Enderl. (4), p. 292, ♀.

♀. Head rather small, globose; frons rugose to coarsely reticulate, transrugose between tubercles, from the anterior of which a strong carina runs longitudinally down frons. Vertex strongly transrugose, behind this a median longitudinal impression, and the occiput finely and closely trans-striate; posterior margin of head bordered. Second flagellar joint one and a half times as long as first; third as long as first and second together. Neck of prothorax strongly, semiannular finely transrugose, posterior margin polished smooth. Mesonotum anteriorly irregularly transrugose, posteriorly coarsely rugoso-punctate; scutellum smooth, apically diffusely punctate. Mesopleuræ smooth, with a transrugose longitudinal impression, the apical third in front of the impression strongly and densely punctate. Metapleuræ and median segment deeply reticulate, scarcely separated. Petiole finely trans-aciculate, apical margin narrowly smooth and polished, longer than rest of abdomen, which is smooth, basally rugose. Terebra longer than body, spicula ferruginous, sheaths black, white-banded before apex. Hind legs with coxæ long and slender, densely trans-striate; femora smooth.

Black; head except vertex and apices of mandibles, and 3-4 basal antennal joints ferruginous; anterior margin of frons and a median streak below anterior tubercle ferruginous; posterior margin of pronotum yellow; anterior legs red-brown; hind tarsi and tibiæ brown. Wings hyaline, nervures pale brown.

Length 14 mm.; abdomen  $9\frac{1}{2}$  mm.; petiole  $5\frac{1}{2}$  mm.; terebra 16 mm.; fore wing  $7\frac{1}{2}$  mm.

Habitat: Soekaranda, Sumatra. 1 ♀. Dr. Dohrn.

Not unlike *D. dohrni* in colour, but petiole and terebra proportionally longer, sheaths of latter white-banded: sculpture of pro- and meso-notum different.



15. *NIGRIPES* Szépl.

*Fenatopus nigripes* Szépl., p. 531, ♀. *Diastephanus n.* Enderl. (2), p. 475.

♀. Frons coarsely rugose; occiput trans-striate with central impression; posterior margin of head bordered. Flagellar joints normal. Neck short and broad, transrugose, semiannular smooth. Mesonotum coarsely rugose; scutellum smooth. Mesopleuræ aciculate, with diffuse large punctures. Median segment with large, more or less confluent punctures, interstices aciculate. Petiole finely trans-striate, as long as rest of abdomen. Terebra as long as body, sheaths white-banded before apex. Hind legs with coxæ transrugose; femora finely aciculate, bidentate.

Black; head and base of antennæ red; middle tibiæ basally and the metatarsus white; hind tibiæ basally red-brown. Wings hyaline, stigma and nervures black.

Length 20 mm.

Habitat: Sumbava, Lesser Sunda Is. Type in Hungarian Nat. Mus., Budapest.

16. *PARVICEPS* Enderl.

*Diastephanus parviceps* Enderl. (4), p. 296, ♀.

♀. Head very small and globose. Frons finely alutaceous (under a 27-power lens it appears finely and densely aciculate); vertex and occiput finely and densely transaciculate, with a sub-obsolete impression behind. Posterior margin of head bordered. Second flagellar joint one and a half times as long as first; third as long as first and second together. Neck granulate aciculate, semiannular smooth; (mesonotum damaged); scutellum polished, with a few marginal punctures on central lobe, lateral lobes finely punctate. Mesopleuræ with a few coarse punctures on anterior half, apex finely and closely punctate. Metapleuræ and median segment coalescent with hexagonal cellular impressions, honey-comb-like. Petiole very finely and closely transaciculate, longer than rest of abdomen, which is smooth, only extreme base of second segment finely punctate rugose. Terebra nearly as long as body, spicula ferruginous, sheaths black, white-banded before apex. Hind coxæ slender, shining, finely and lightly trans-striate; hind femora shining smooth, with microscopic reticulations.

Black; head (except apices of mandibles, vertex, and frons to anterior tubercle, which are black-brown), base of antennæ, front tarsi, middle tibiæ and tarsi ferruginous-yellow; hind tibiæ and tarsi brown. Wings hyaline, nervures brown; stigma very long and narrow, hyaline.

Length 11 mm.; abdomen  $6\frac{3}{4}$  mm.; petiole  $3\frac{3}{4}$  mm.; terebra  $10\frac{1}{2}$  mm.; fore wing 6 mm.

Habitat: Soekaranda, Sumatra. 1 ♀. Dr. Dohrn.

## 17. FRONTILINEA Morley.

*Diastephanus frontilinea* Morley (1), p. 109, ♀.

♀. Frons finely reticulate and white pubescent; vertex longitudinally aciculate; occiput very finely and closely trans-aciculate; frontal tubercles prominent and acuminate, the anterior rather larger. Posterior margin of head reflexed. Antennæ with first and second flagellar joints of equal length and rather shorter than third. Neck multicarinate, semiannular smooth and shining. Mesonotum very short, shining and sparsely punctate. Scutellum large and flat, with the impressions marked only by two rows of three punctures in front, smooth and shining. Mesopleuræ finely alutaceous and pubescent, with a few scattered punctures; metapleuræ smooth and finely subaciculate, separated by a strongly-marked sulcus from the median segment, which is coriaceous between very large and partly confluent punctures. Petiole transaciculate, longer than rest of abdomen; second segment basally narrowly scabrous, remainder of abdomen smooth; apex of sixth segment discally acutely emarginate. Terebra shorter than body, sheaths white-banded before apex. Hind legs with coxæ trans-striate; femora alutaceous, bidentate; tibiæ as long as femora, compressed to a little beyond middle and there internally excised.

Black; mouth-parts, inner and outer orbits testaceous; a longitudinal line down centre of frons and the tubercles rufous; anterior tibiæ testaceous and hind tarsi red. Wings narrow, hyaline; stigma lanceolate and subhyaline.

Length  $10\frac{1}{2}$  mm.; abdomen  $5\frac{1}{2}$  mm.; petiole 3 mm.; terebra 9 mm.

Habitat: Rangpur, on border of Eastern Bengal and Assam; 25. vii. 05. Type in Pusa collection.

## 18. TRILINEATUS Elliott.

*Diastephanus trilineatus* Elliott (3), p. 81, ♀.

♀. Frons and vertex very finely arcuate striate, occiput trans-striate; carinæ between posterior ocelli subobsolete; posterior margin of head bordered. Second flagellar joint half as long again as first; third as long as first and second together. Pronotum trans-striate; mesonotum diffusely punctate; scutellum smooth. Propleuræ smooth; mesopleuræ finely striate and punctate; metapleuræ and median segment cribrate punctate. Petiole trans-striate, apically smooth, as long as the smooth remainder of abdomen. Terebra shorter than body, with subapical white band. Hind coxæ trans-striate, their femora bidentate; tibiæ compressed slightly beyond middle.

Black; mouth-parts flavous, inner and outer orbits and frons centrally and two basal joints of antennæ flavous; vertex and occiput nigro-rufescent; legs more or less rufescent. Wings hyaline.

Length 9-13 mm.; abdomen 5-8 mm.; petiole  $2\frac{1}{2}$ -4 mm.; terebra  $8\frac{1}{2}$ -12 mm.

Habitat: Hoabinh, Tonkin. R. V. de Salvaza; Aug. 1918. Two specimens in the British Museum.

The colour of the head in this species is exactly as in *D. bilineatus* Elliott, from which it differs in the bidentate hind femora and concolorous teeth.

#### 19. CHINENSIS Elliott.

*Diastephanus chinensis* Elliott (2), p. 73, ♀.

♀. Frons very finely striate, transversely below, becoming longitudinal above, round the anterior tubercle and in the ocellar space; vertex and occiput finely longitudinally striate; posterior margin of head bordered. Basal flagellar joints normal. Pronotum trans-striate, semiannular more coarsely, especially laterally. Mesonotum coarsely punctate; central lobe of scutellum with diffuse large punctures, lateral lobes with the external half longitudinally striate. Propleuræ longitudinally striate above and smooth beneath; mesopleuræ alutaceous; metapleuræ coarsely punctate above, trans-striate beneath, separated by a carina from the cribrate-punctate median segment. Petiole finely trans-striate, with extreme apex smooth, as long as rest of abdomen, which is smooth and shining. Terebra slightly longer than body, spicula rufescent, sheaths black, with subapical white band. Hind coxæ trans-striate; hind femora finely alutaceous and shining, bidentate; tibiæ compressed to beyond middle, alutaceous, the explanate part less strongly sculptured.

Black; head except vertex, two basal antennal joints and the anterior legs rufescent. Wings hyaline, nervures brown.

Length 12 mm.; abdomen 8 mm.; petiole 4 mm.; terebra 13 mm.

Habitat: China; Haut Mékong, Tong King. R. V. de Salvaza. Type in British Museum.

Distinguished by the sculpture of the frons and vertex, and especially by the striation of the outer lobes of the scutellum.

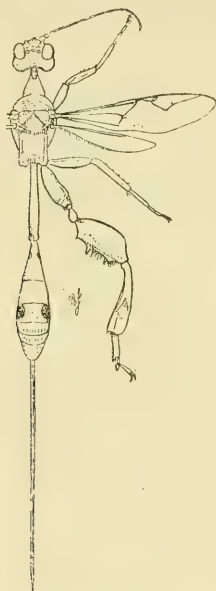
#### 20. ALUTACEUS Morley.

*Diastephanus alutaceus* Morley (1), p. 109, ♀.

♀. Body entirely alutaceous and dull throughout. Head finely transrugose in front; all frontal tubercles small; vertex with one carina behind basal tubercle; a few weak transcarinae at posterior margin of occiput, which is bordered. Antennæ as long as head and thorax; second flagellar joint one and a half times as long as first; third only as long as second; all flagellar joints well discreted *inter se*. Neck with a discal longitudinal sulcus, apically only laterally transcarinate, semiannular basally explanate. Scutellum as broad as long, apically obtuse, the

usual impressions or rows of punctures are wanting. Mesopleuræ smoothened than mesonotum and pubescent; metapleuræ confluent with median segment, which is explanate and slightly transcarinate immediately before its apex. Petiole shorter than the remaining segments, second basally constricted, sixth apically discally emarginate. Terebra shorter than body. Hind coxæ as long as femora, which are strongly incrassate, bidentate, and basally angulate below; tibiæ longer than femora, compressed to middle and there excised.

Text-figure 6.



*Diastephanus alutaceus*.

Rufo-testaceous; eyes, ocelli, apex of mandibles, frenum, spot at base of petiole, circular spot on each side of basal third of second segment, and a larger spot on each side of fourth black; femoral teeth white; terebra rufo-testaceous, apically black. Wings lacteous-hyaline, with a circular pale fuscous spot in the discoidal cell, and another very faint one below the centrally infusate stigma.

Length 10 mm.; abdomen 6 mm.; petiole  $2\frac{1}{2}$  mm.; terebra 8 mm.

Habitat: Lonely Mine, Rhodesia. H. Swale, 12.v.1914. Type in British Museum.

21. *BREVIPETIOLATUS* Enderl.

*Stephanus brevipetiolatus* Enderl. (1), p. 205, ♀. *Dia-stephanus b.* Enderl. (2), p. 475.

♀. Head small; frons finely arcuate rugose; anterior tubercle very long and pointed, the four others indistinct. Vertex coarsely transrugose; occiput finely and closely punctate, slightly rugose; posterior margin of head bordered. First and second flagellar joints of equal length, third and fourth also equal, and twice as long as first. Pronotum smooth and dull. Mesonotum irregularly transrugose; scutellum centrally dull, not punctate, the anteriorly convergent rows of punctures deep. Meso- and meta-pleuræ and median segment finely alutaceous, latter not separated from metapleuræ. Petiole dull, only apically sub-transrugose, stout, clavate, and only half as long as remainder of abdomen. Terebra as long as body, spicula yellow, sheaths brown. Hind coxæ finely trans-striate.

Black; frons, vertex, and apex of mandibles black; remainder of head, four basal antennal joints, and band at base of third segment ferruginous; legs ferruginous, femora basally and above and hind tibiæ centrally black. Wings hyaline, nervures pale brown.

Length 8 mm.

Habitat: Johann Albrechtshöhe, North Cameroons. L. Conradt.

The unusually short and stout petiole, together with the dull pronotum and scutellum, distinguish this species from all others.

The group of species, including *D. schlettereri*, *togoensis* and its var. *fasciatus*, *flavomaculatus*, and *brevipetiolatus*, all from Johann Albrechtshöhe, have much in common, and require further elucidation.

22. *TRILOBATUS* Elliott.

*Diastephanus trilobatus* Elliott (3), p. 32, ♀.

♀. Frons and vertex extremely finely, occiput more coarsely trans-striate; posterior margin of head very finely bordered. Scape slightly longer than cheeks. First and second flagellar joints of equal length, third about as long as first and second together. Pronotum transrugose, apically coarsely, basally more finely, with extreme base smooth; mesonotum and scutellum smooth, with a few coarse punctures; mesopleuræ smooth above, punctate below; metapleuræ cribrate punctate; median segment coarsely and irregularly punctate. Petiole shorter than rest of abdomen, finely trans-striate, remaining segments smooth. Terebra very slightly longer than body, sheaths black. Hind coxæ basally punctate, remainder trans-striate; femora bidentate; tibiæ compressed to beyond middle.

Black; head beneath, inner orbits, and frons flavous; the



upper margin of the colour is trilobed, the central lobe extending to the lower tubercle, the outer lobes triangular; antennæ basally rufo-testaceous; posterior metatarsi white. Wings hyaline.

Length 11 mm.; abdomen 7 mm.; petiole 3 mm.; terebra  $11\frac{1}{2}$  mm.

Habitat: Hoabinh, Tonkin. R. V. de Salvaza. Aug. 1918. Type in British Museum.

Differs from *D. trilineatus* Elliott in the shorter second flagellar joint, sculpture of mesonotum and mesopleuræ, and black terebral sheaths. In *D. trilineatus* and *simillimus* two descending rufescent streaks divide the space between the eyes into five about equally broad strips of colour, and the lower tubercle is entirely black. In *D. trilobatus* the narrow central streak extends to the top of the tubercle and the outer streaks are broadly triangular.

### 23. DOHRNI Enderl.

*Diastephanus dohrni* Enderl. (4), p. 291, ♀.

♀. Head medium size; frons anteriorly regularly, posteriorly irregularly transrugose, an irregular longitudinal impression below anterior tubercle, space between tubercles arcuate rugose; vertex transrugose; occiput rather wavily trans-striate with central longitudinal impression and finely bordered. Second flagellar joint one and a half times as long as first; third as long as first and second together. Pronotum dull, indistinctly transrugose in front, posterior margin polished smooth. Mesonotum smooth, with diffuse coarse punctures and apically transrugose; scutellum smooth, six deep punctures on each side. Mesopleuræ smooth, anterior third densely and finely punctate, with diffuse larger punctures, posterior half coarsely punctate on each side of a central carina. Metapleuræ and median segment coalescent, irregularly and laterally reticulately punctate. Petiole finely trans-striate, apically transrugose, shorter than rest of abdomen, which is smooth, basally slightly rugose. Terebra as long as body, spicula red-yellow, sheaths entirely black. Hind legs with coxæ slender, finely and densely trans-striate; femora smooth, with microscopic sculpture.

Black; head except vertex and apices of mandibles, 4-5 basal antennal joints ferruginous; anterior legs pale ferruginous, hind tibiæ and tarsi dark brown. Wings hyaline; nervures brown, stigma hyaline, apically very pointed.

Length 18 mm.; abdomen  $11\frac{1}{2}$  mm.; petiole  $5\frac{1}{2}$  mm.; terebra 18 mm.; fore wing  $9\frac{1}{2}$  mm.

Habitat: Soekaranda, Sumatra. 1 ♀. Dr. Dohrn; Jan. 1894.

This species is not unlike *D. carinifrons* Enderl. in colour and in habitus, but differs chiefly in the structure and sculpture of head, shorter petiole and terebra, the latter having entirely black sheaths.

24. *QUADRIDENS* Elliott.

*Diastephanus quadridens* Elliott (3), p. 31, ♀.

♀. Frons strongly arcuate rugose, vertex and occiput strongly trans-striate and sulcate; three carinæ between posterior ocelli; ocellar space rugose; posterior margin of head bordered. Second flagellar joint one and a half times as long as first; third as long as first and second together. Prothorax coarsely trans-striate, basally more finely and extreme base smooth; mesothorax trans-rugose; marginal punctures of scutellum deep. Propleuræ finely striate; mesopleuræ punctate above, smooth beneath; metapleuræ and median segment strongly cribrate punctate. Petiole finely trans-striate, as long as remaining smooth, shining segments. Terebra longer than body, sheaths black. Hind coxæ and femora densely and finely trans-striate, latter bidentate, but the two prominences on basal half so unusually developed as almost to rank as teeth; tibiæ compressed to middle.

Black; head and two basal antennal joints rufo-testaceous; vertex nigrescent. Wings hyaline.

Length 15 mm.; abdomen 10 mm.; petiole 5 mm.; terebra 17 mm.

Habitat: Luang Prabang, Indo-China. R. V. de Salvaza; 5.x.1917. Type in British Museum.

This species is characterized by the unusual development of the femoral subsidiary tubercles, as well as by the sculpture of the prothorax, mesopleuræ, hind coxæ, and femora.

25. *TEREBELLUS* Enderl.

*Stephanus terebellus* Enderl. (1), p. 204, ♀. *Diastephanus* (2), p. 475.

♀. Head small; frons arcuate rugose, vertex coarsely, occiput finely transrugose; posterior margin of head sharply bordered. First and second flagellar joints of equal length, third and fourth also equal and each twice as long as first. Pronotum elongate, polished smooth, punctured only in front and round scutellum, which is polished smooth. Metanotum very narrow, coarsely longitudinally rugose. Mesopleuræ polished smooth above, densely pubescent and diffusely punctate below; metapleuræ diffusely, posteriorly more densely punctate, separated by a slightly raised costa from the median segment, which is finely alutaceous, laterally diffusely punctate, with a fine longitudinal median line. Petiole finely trans-striate, about as long as rest of abdomen. Terebra only half as long as body, sheaths black, apically ferruginous. Hind coxæ finely trans-striate.

Black; face, cheeks, temples, 5 basal antennal joints, anterior femora, hind femora beneath, third and fourth sternites ferruginous. Wings hyaline; stigma and nervures pale yellowish. Antennæ from sixth joint brown; hind metatarsus whitish.

Length  $8\frac{1}{2}$  mm.

Habitat: Lolodorf, South-East Cameroons. L. Conradt.

This species appears to be characterized by the small head, smooth pro- and meso-thorax, and very short terebra.

26. *RUFICOLLIS* Enderl.

*Diastephanus ruficollis* Enderl. (3), p. 205, ♀ ♂.

♀ ♂. Head small, globose. Neck strongly transrugose, laterally more finely; semiannular trans-striate, basally more coarsely and posterior margin laterally irregularly rugose. Mesopleuræ dull, with large diffuse punctures, upper third finely granulate punctate, yellow pubescent. Petiole very slender, finely trans-striate; second segment dull, finely punctate, basally more granulate. Terebra in ♀ slightly shorter than body, sheaths entirely black. Hind femora bidentate; hind coxæ smooth, hind tibiæ and metatarsus without pubescence.

Black; head ferruginous yellow, vertex more brown in ♀, redder in ♂; antennæ darkish rufo-testaceous, apically brown; posterior half of pronotum ferruginous; anterior coxæ and legs pale ferruginous, all tarsi rufescent. Anterior femoral tooth yellow, the posterior black. Wings hyaline; stigma long and yellow, nervures brown.

Length, ♀,  $10\frac{1}{2}$  mm.; petiole 3.2 mm.; terebra  $10\frac{1}{2}$  mm.; fore wing 6 mm. ♂, 8 mm.; petiole 2.2 mm.; fore wing 4.4-4.6 mm.

Habitat: Formosa. H. Sauter; May-June 1912. Co-types in Dahlen and Stettin Museums.

Differs from *D. flavidentatus* in the entirely yellowish head, not pubescent hind tibiæ and metatarsus, black terebral sheaths and black posterior femoral tooth.

27. *MACULIFEMUR* Enderl.

*Diastephanus maculifemur* Enderl. (4), p. 294, ♀.

♀. Head rather large, globose. Frons densely and coarsely punctato-rugose, the rugosities run from the median line obliquely backwards, apically more transversely; space between frontal tubercles longitudinally striate; vertex with three or four strong transcarinæ; occiput wavily trans-striate and finely punctate, with narrow central impression. Cheeks buccate; posterior margin of head bordered. Second flagellar joint one and a half times as long as first; third almost longer than first and second together. Pronotum densely trans-striate, more strongly towards apex, posterior margin polished smooth. Mesonotum apically strongly transrugose, dorsally with deep diffuse punctures and microscopic striation, a deep impression before scutellum, which is polished smooth, with deep marginal punctures and subobsolete median impression. Mesopleuræ polished smooth, diffusely punctate beneath, apically finely and densely punctate; metapleuræ and median segment separated by a carina between two rows of small punctures, and both with large hexagonal to circular punctures, honeycomb-like. Petiole very

finely and densely transaciculate, with narrow smooth posterior margin, about as long as remainder of abdomen, which is smooth, basally finely rugoso-punctate. Terebra shorter than body, spicula ferruginous, sheaths entirely black. Hind coxæ slender, shining, very finely transaciculate; hind femora smooth, shining, with microscopic reticulations, bidentate.

Black; head except apices of mandibles, and three basal antennal joints ferruginous; posterior margin of pronotum yellow-brown. Basal fourth of intermediate tibiae, basal half of their metatarsus, a small elongate oval spot near apex of hind femora outside, and the femoral teeth white. Wings hyaline, nervures brown; stigma very long and narrow, yellow hyaline.

Length  $13-15\frac{1}{2}$  mm.; abdomen  $7\frac{1}{2}-8\frac{1}{2}$  mm.; petiole  $3\frac{1}{2}-4\frac{1}{2}$  mm.; terebra  $10-12$  mm.; fore wing  $7\frac{1}{2}-8\frac{1}{2}$  mm.

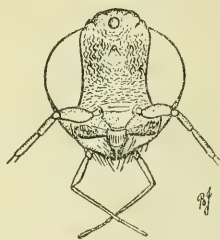
Habitat: Perak, 1 ♀; Malacca, 1 ♀.

Text-figure 7.



*Diastephanus sulcatus*.

Text-figure 8.



*Diastephanus sulcatus*.

## 28. SULCATUS Elliott.

*Diastephanus sulcatus* Elliott (3), p. 80, ♀.

♀. Face irregularly rugose, vertex and occiput trans-striate, with very distinct longitudinal sulcus; three stout, curved carinae between the posterior ocelli; posterior margin of head bordered. Scape longer than cheeks. Basal flagellar joints



normal. Neck finely trans-striate, semiannular smooth in front, basally arcuate striate; mesonotum rugose; scutellum laterally strongly punctate; metanotum longitudinally carinate. Propleuræ smooth; mesopleuræ finely trans-striate, apically punctate; metapleuræ and median segment cribrate punctate, the latter with an elongate triangular central basal punctate and very finely trans-striate and dull space, bounded by large punctures. Petiole trans-striate, shorter than the remaining smooth segments. Terebra shorter than body, spicula pale red, sheaths black. Hind coxæ finely trans-striate, their femora glabrous, bidentate; tibiæ compressed to middle.

Black; head red, apices of frontal tubercles and the carina on the vertex black; two basal antennal joints rufo-testaceous, third darker red, apically black. Anterior tibiæ and all tarsi rufescent; femoral teeth white. Wings hyaline.

Length 13 mm.; abdomen  $7\frac{1}{2}$  mm.; petiole  $3\frac{1}{2}$  mm.; terebra 11 mm.

Habitat: Luang Prabang, Indo-China. H. V. de Salvaza; 29. ix. 1917. Type in the British Museum.

The sculpture of the median segment resembles that of *D. leucodontus* Schlett., which the author describes as "basally and centrally smooth," and agrees also in the colour of the head and of the femoral teeth. It differs in sculpture of head and prothorax and black terebral sheaths.

## 29. SALOMONIS Westw.

*Stephanus salomonis* Westw. (5), p. 128, ♀. *Diastephanus s.* Morley (1), p. 107; Brues, p. 100; Elliott (2), p. 74, ♀.

♀. Frons and occiput arcuately rugose, latter with slight longitudinal sulcus; posterior margin of head bordered. Second and third flagellar joints of equal length, and about one-third longer than first. Neck elongate, glabrous, centrally deeply impressed and laterally vallyately elevated; semiannular smooth, with a few apical transcarinæ, and a band of indistinct punctures before the base. Mesonotum rather densely punctate; mesopleuræ subglabrous, with a few superficial punctures; median segment with large, rather dense, but not confluent punctures. Petiole rather longer than rest of abdomen, trans-striate; second segment basally constricted and slightly rugulose, remaining segments smooth. Terebra slightly shorter than body, sheaths entirely black. Hind coxæ trans-striate, hind femora alutaceous, shining, bidentate; hind tibiæ compressed to middle.

Black; face below antennæ, inner orbits partly, outer orbits entirely pale stramineous; mandibles and anterior legs bright ferruginous; hind legs with coxæ, base of femora and apex of tibiæ more or less black. In the type-specimen the basal half



of the hind femora is black all over, but in the other above only. Wings hyaline.

Length 16 mm.; abdomen 10 mm.; petiole  $5\frac{1}{2}$  mm.; terebra 15 mm.

Habitat: Solomon's Island, New Hebrides (Westwood); Solomon Islands (Woodford).

The specimen described by Westwood, now in the British Museum, was taken during the voyage of H.M.S. 'Herald' in 1866. The abdomen is wanting, but the three-jointed tarsi prove it to be a female. In the same collection is a perfect specimen, taken by C. M. Woodford, probably about 1886, from which the description has been completed.

The extraordinarily deeply-excised neck of pronotum is very distinctive of the species; I know of no other at all like it.

Mr. T. C. Brues (*l. c.*) describes a specimen from Wai-ai, Solomon Is., which he considers to be this species. It differs in colour, in the legs being entirely black, except apical half of hind femora and basal constricted part of their tibiae, second flagellar joint rather longer. The peculiar formation of the neck is not noted, but it is said to be finely trans-rugose, mesonotum irregularly rugose-reticulate in front, smooth behind. Allowing for the personal equation in descriptions, and the common variation in the colour of the legs in insects, I think the specimen described is truly this species.

Schletterer (p. 123) tentatively synonymizes this species with his *D. pallescens* from the Philippines; from it, however, *D. salomonis* differs in the above-named formation of the prothorax, the proportionate length of the basal antennal joints, and in having bidentate hind femora; these in *D. pallescens* are tridentate.

### 30. CELEBENSIS Szépl.

*Fœnatopus celebensis* Szépl., p. 531, ♀. *Diastephanus* Enderl. (2), p. 475.

♀. Frons coarsely and indistinctly transrugose; occiput finely transrugose, with indistinct central impression; posterior margin of head bordered. Flagellar joints normal. Neck elongate, smooth in front, feebly trans-striate behind; mesonotum and scutellum smooth; mesopleuræ smooth, anteriorly rugose-punctate. Median segment cribrate punctate. Petiole finely trans-striate, nearly as long as rest of abdomen. Terebra rather shorter than body, sheaths black. Hind legs with coxæ finely transrugose; femora shining, extremely finely alutaceous, bidentate.

Black; temples, cheeks, and inner orbits yellowish; mouth, a median stripe on frons, and base of antennæ yellow-red; anterior tibiae, basal half of hind tibiae, and the tarsi brown-red. Wings hyaline, stigma centrally yellowish, tegulae brownish.

Length 16 mm.

Habitat: Toli-Toli, North Celebes. Type in Hungarian National Museum, Budapest.

31. *SZEPLIGETII* Enderl.

*Diastephanus szepligetii* Enderl. (2), p. 476, ♀.

♀. Frons irregularly rugose; vertex with two transcarinae; occiput densely granulate rugose. Temples inflated. Scape shorter than second flagellar joint, which is scarcely twice as long as first; third and fourth of equal length and shorter than first and second together. Pronotum polished smooth; propleuræ very finely punctate in front, centrally finely and densely aciculate, smooth behind, separated from pronotum by a deep sulcus. Mesonotum dull, diffusely punctate, anteriorly rugose. Scutellum smooth, with large diffuse marginal punctures. Mesopleuræ rugose and finely punctate; metapleuræ coarsely reticulate rugose, separated by a longitudinal carina from median segment, which is somewhat smooth, diffusely and deeply punctate, apically rugose. Abdomen rough, finely and densely punctate; petiole shorter than rest of abdomen. Terebra shorter than body (sheaths broken). Hind coxæ finely and densely punctate, posteriorly finely striate.

Black; head ferruginous, except apices of mandibles, vertex, and occiput; scape, first flagellar joint, apices of femora, tibiæ and tarsi except last tarsal joint, ferruginous. Wings hyaline, stigma brown-yellow, nervures golden-brown.

Length 15 mm.; abdomen 9 mm.; petiole  $3\frac{1}{2}$  mm.; spicula 13 mm.; fore wing 8 mm.; expanse of wings  $17\frac{1}{2}$  mm.

Habitat: Sierra Leone, West Africa.

32. *SIMILLIMUS* Elliott.

*Diastephanus simillimus* Elliott (3), p. 82, ♀.

♀. Head extremely finely trans-striate; flagellar joints normal. Neck rather finely trans-striate, semiannular smooth; mesonotum punctate; mesopleuræ smooth above, punctate beneath; median segment and metapleuræ cribrate punctate. Petiole very finely trans-striate, slightly longer than the remaining smooth segments. Terebra much shorter than body, sheaths black. Hind coxæ trans-striate; femora smooth, bidentate; tibiæ compressed to middle.

Black; front of head coloured exactly as in *D. trilineatus* Elliott, to which it bears a strong resemblance. Wings hyaline.

Length  $12\frac{1}{2}$  mm.; abdomen  $7\frac{1}{2}$  mm.; petiole 4 mm.; terebra 9 mm.

Habitat: Hoabinh, Tonkin. Aug. 1918; R. V. de Salvaza.

This species appears to differ from *D. trilineatus* Elliott chiefly in the proportional length of the second flagellar joint, in sculpture, and in the entirely black terebral sheaths. Type in British Museum.

33. *SIMILIS* Szépl.

*Fœnatopus similis* Szépl., p. 530, ♂. *Diastephanus*, Enderl. (2), p. 475.

♂. Frons finely alutaceo-rugose; occiput short and rugose; posterior margin of head bordered. First and second flagellar joints of equal length. Neck short, finely rugose, dull, semi-annular coarsely rugose, as is also the mesonotum. Scutellum diffusely punctured, centrally smooth. Mesopleuræ finely rugose, not punctate; median segment with large, but not confluent, punctures. Petiole finely trans-striate, about as long as remainder of abdomen. Hind legs with coxæ finely trans-striate; femora finely and densely punctate, tridentate; tarsi four-jointed.

Black; head ferruginous, vertex nigrescent, temples and cheeks yellowish; anterior legs except middle coxæ and the hind tarsi yellow-red. Wings hyaline; stigma and nervures brown.

Length 11 mm.

Habitat: Simbang, New Guinea. Type in Hungarian National Museum, Budapest.

This species closely resembles *D. birói* Szépl. from the same locality, and may prove to be the male of that species.

Szépligetti states that in this species, in *D. fasciatus* ♂, and in *H. wiistneii* ♂ the hind tarsi are four-jointed. This is undoubtedly an error, as the said tarsi are five-jointed in all other known males, excepting only *S. tibiator* Schlett., in which they are three-jointed as in the typical female.

34. *FLAVICEPS* Elliott.

*Diastephanus flaviceps* Elliott (1), p. 131, ♂.

♂. Frons alutaceous, dull; vertex and occiput in front arcuate rugose, becoming transverse towards posterior margin, which is simple. First and second flagellar joints of equal length, third a little longer. Prothorax almost smooth; mesonotum trans-striate in front, central row of punctures and lateral impressions distinct; median segment coarsely punctate. Petiole trans-striate, a little longer than rest of abdomen; which is smooth and shining. Hind coxæ trans-striate; femora smooth, tridentate; tibiæ compressed to beyond middle.

Black; face, frons, base of antennæ, and anterior legs testaceous; cheeks pale red, occiput dark red; apex of prothorax and the hind femora rufescent. Wings hyaline.

Length 11 mm.; abdomen  $7\frac{1}{2}$  mm.; petiole 4 mm.

Habitat? The type in the British Museum bears a label "F. Sm. coll. 79. 22." without locality.

35. *FUSCINERVIS* Cam.

*Fœnatopus fuscinervis* Cam. (4), p. 101, ♂.

♂. Frons rugose-punctate, laterally closely trans-striate;

vertex closely trans-striate, as also the occiput, which has an indistinct longitudinal impression. Anterior three frontal tubercles stout, conical; the posterior smaller and more rounded. Second flagellar joint not quite twice as long as first. Pronotum closely aciculate, basally smooth, with an apical transcarina. Mesonotum centrally trans-striate; scutellum smooth. Mesopleuræ basally and apically sparsely punctate; metapleuræ reticulate, lower half smooth, with four suboblique carinæ. Median segment strongly reticulate. Petiole closely trans-striate, nearly twice as long as rest of abdomen, which is short ovate. Hind legs with coxæ finely trans-striate; femora rather dull, basally transrugose, tridentate; tibiæ compressed to middle.

Black; head dark red, vertex nigrescent, outer orbits yellow; pronotum basally, second and third abdominal segments laterally testaceous; anterior coxæ, trochanters, tibiæ and tarsi rufo-testaceous; hind tarsi red. Wings hyaline; stigma and nervures pale fuscous.

Length 12–14 mm.; abdomen  $5\frac{1}{2}$ –7 mm.; petiole  $3\frac{1}{2}$ – $4\frac{1}{2}$  mm.

Habitat: Kuching, Sarawak. Type in British Museum.

### 36. FLAVIFRONS Elliott.

*Diastephanus flavifrons* Elliott (1), p. 131, ♂.

♂. Frons irregularly rugose, vertex transcarinate, occiput trans-striate; posterior margin of head bordered. Second flagellar joint nearly twice as long as first; third not quite as long as first and second together. Pronotum trans-striate, deeply impressed at apex; mesonotum centrally smooth, laterally rugose, lateral impressions distinct. Mesopleuræ finely striate; metapleuræ punctate; median segment coarsely punctate. Petiole trans-striate, as long as rest of abdomen, which is smooth and shining. Hind coxæ trans-striate; hind femora smooth, bidentate.

Black; face and lower half of frons white, the edges of the colour sharply defined, that of the black forming an inverted W, and the mandibles apically broadly black, sharply defined; frontal tubercles rufescent; two basal antennal joints pale red; apex of pronotum obscurely, second and third abdominal segments, anterior tibiæ and tarsi rufescent. Wings hyaline, with red and green iridescence.

Length 11 mm.; abdomen 8 mm.; petiole 4 mm.

Habitat: Quop, West Sarawak. G. E. Bryant; iv. 1914. Type in British Museum.

This species is distinguished by the colour of the head; the black colour of the mandibles, which is unusually broad, has a straight margin against the white of the face, while the lower border of the dark upper part of frons forms a clear-cut broad inverted W.



37. *FASCIATUS* Szépl.

*Fænatopus fasciatus* Szépl., p. 529, ♂. *Diastephanus* Enderl. (2), p. 475.

♂. Frons finely and distinctly transrugose; occiput short and transrugose; posterior margin of head bordered. First flagellar joint subglobose, little shorter than second. Pronotum elongate, slender, transrugose. Mesonotum and scutellum nearly smooth. Mesopleuræ anteriorly finely rugose, indistinctly punctate. Median segment with large, superficial, and not very dense punctures, interstice alutaceous. Petiole densely trans-striate, longer than rest of abdomen. Hind coxæ densely and irregularly transrugose; hind femora finely alutaceo-punctate, dull, bidentate; hind tarsi four-jointed.

Black; head except vertex, base of antennæ, prosternum, anterior legs, hind femora centrally, hind tarsi, and apical angles of second segment yellow-red; tegulæ flavous, with black spot. Wings hyaline, nervures yellow-brown, stigma centrally flavous.

Length 9 mm.

Habitat: Sumbava. Type in Hungarian National Museum, Budapest.

38. *FLAVONOTATUS* Elliott.

*Diastephanus flavonotatus* Elliott (2), p. 32, ♂.

♂. Frons extremely finely transversely coriaceo-rugose; vertex with four carinæ; occiput short, finely trans-striate, its posterior margin simple. Anterior frontal tubercle almost obsolete. Scape a little shorter than cheeks. Second flagellar joint one and a half times as long as first. Neck elongate and slender, the whole pronotum obsoletely trans-striate, becoming subnitidulous basally, with a short longitudinal fovea. Scutellum smooth; mesonotum nearly smooth. Pro- and meso-pleuræ smooth, the latter diffusely punctate; metapleuræ smooth in front, reticulate rugose behind; median segment coarsely punctate. Petiole very finely trans-striate, shorter than the remaining strongly nitidulous segments. Hind coxæ slender, trans-striate; their femora smooth, with two large white teeth; tibiæ compressed to beyond middle.

Black; frons flavous, vertex ferruginous, occiput nigrescent. Antennæ testaceous; pronotum subrufescent. Anterior legs rufo-testaceous. Hind coxæ black, femora ferruginous, centrally paler; tibiæ darker, apically and the metatarsus flavous, other tarsal joints rufescent. Petiole black, remaining segments rufescent, a large circular flavous mark on each side of third segment near base. Wings hyaline, iridescent; nervures pale fuscous.

Length  $19\frac{1}{2}$  mm.; abdomen  $6\frac{1}{2}$  mm.; petiole 3 mm.

Habitat: Kuching, Sarawak. 14.v.1900. Type in British Museum.



This may prove to be the male of *D. leucodontus* Schlett., also from Sarawak, with which it agrees in the obsolete frontal tubercle, short occiput, and very largely in sculpture. The round flavous spots on third segment are very distinctive, and I do not feel sure enough of the connection to unite them.

#### DOUBTFUL SPECIES.

The following species cannot be placed, in consequence of defective descriptions :—

##### MEGISCHUS CANADENSIS Davis.

*Megischus canadensis* Davis, Trans. Amer. Ent. Soc. xxiv. p. 349 (1897), ♀.

“♀, 14 mm., ovipositor 18 mm.

“Black, with cheeks beneath and posterior tarsi dirty yellow; four anterior legs with tibiæ, tarsi and apical trochanter, also hind trochanters, pale piceous; wings hyaline, nervures and stigma reddish-brown: the sculpturing is different from and much finer than in the preceding species (*M. floridanus*, see below), the head, including face, is circularly reticulate, very finely so on the occiput; prothorax coarsely reticulate; petiole irregularly transversely wrinkled; five spines of the head are mere transverse prominences and the anterior ocellus is in a broad, rather deep basin; guides of ovipositor broken.

“One specimen from Toronto, Canada, collected July 15th by Mr. T. C. Priddey.”

##### STEPHANUS DIADEMA Fab.

*Fœnus diadema* Fab. MSS. Type in Mus. Kiliæ.

*Stephanus diadema* (Fab.), Westw. Trans. Ent. Soc. Lond. iii. p. 277 (1843).

“I am unfortunately unable to determine whether this undescribed insect be specifically different from the last (*S. bicolor*); the notes which I made at Kiel simply stating that the ænus diadema of the Fabrician cabinet is a *Stephanus* with a red head.”

There appears to be no other reference to this species, though the name appears in all lists of Stephanidæ.

##### STEPHANUS DIVERSUS Schlett.

*Megischus furcatus* Brullé, Hist. Nat. Ins. Hym. iv. p. 539 (1846); Westw. Trans. Ent. Soc. Lond. 1850-51, p. 228, ♀. *Stephanus diversus* Schlett. Berl. Ent. Zeit. xxxiii. p. 133 (1889), ♀.

“Niger, alis fere fuscis, abdominis segmento secundo lævigato, valvulis terebræ nigris. Fem.

“Il est noir, avec les joues roux et la base des mandibules d’un

roux ferrugineux. Les ailes sont lavées de bistre et leurs nervures sont noires. Cette espèce ressemble beaucoup à la précédente (*annulator*=*furcatus* Lep. & Serv.). Elle n'en diffère, pour ainsi dire, que par sa taille moindre, par la couleur plus foncée de ses ailes et par les valves de sa tarière qui sont plus grêles, sans anneau blanc, et dont l'extrémité n'est pas lanceolée comme dans *Meg. annulator*. Long. du corps 0·030, de la tarière 0·040. *Hab.* le Brésil; collect. de M. Serville.

"Le nom *furcatus*, qui porte cette espèce, vient sans doute de ce que le prothorax est échancré en avant. Cette disposition existe dans le *M. annulator*, dont la partie antérieure du prothorax est d'un roux ferrugineux."

Schletterer writes:—"Brullé has described under the name of *annulator*, a species previously named *furcatus* by Lepeletier and Serville in 1825. His *furcatus*, which is sufficiently distinguished from *furcatus* Lep. & Serv. by the entirely black terebral sheaths and darker wings, must be re-named: I call it *diversus*."

#### MEGISCHUS FLORIDANUS Davis.

*Megischus floridanus* Davis, Trans. Amer. Ent. Soc. xxiv. p. 349 (1897), ♀ ♂.

"♀ ♂—♀ 20 mm., ovipositor 22 mm.; ♂ 6 mm.

"Black, with head, thorax, and tarsi slightly reddish, decidedly so in ♂; guides of the ovipositor in ♀ with a broad white band near the apex; wings yellowish fusco-hyaline, nearer hyaline in ♂; front, vertex, hind coxæ, and petiole strongly rugose and more or less reticulate, distinctly so on vertex and prothorax, and in ♀ on petiole, becoming finer towards apex; front above antennæ very rough and with five tubercles distinct, the last two placed between the hind ocelli; heel segment of hind tarsus with large, dense scopal pads.

"Two specimens from Florida, collected by Mr. T. C. Priddey."

#### STEPHANUS FRONTALIS Klug, Westw.

*Stephanus frontalis* Klug, MSS.; Westw. Trans. Ent. Soc. Lond. iii. p. 276 (1843) (sine descript.).

"Species adhuc inedita, in Mus. Reg. Berolinensis conserv. Habitat Caput Bonæ Spei."

#### STEPHANUS SPOLIATOR Smith.

*Megischus spoliator* Smith, Journ. Proc. Linn. Soc. Lond. vii. p. 6 (1884), ♀. *Stephanus spoliator* Schlett. Berl. Ent. Zeit. xxxiii. p. 117 (1889), ♀.

"*M. niger*, mandibulis et antennarum basi rufis; thorace rugose; pedibus anticis et intermediis ferrugineis, tarsis posterioribus rubris; alis hyalinis.

"*Female*. Length 7 lines. Black; the mandibles, palpi, and five basal joints of the antennæ ferruginous; the face rugose, the

front with three short acute tubercles placed in a triangle, behind which the head is transversely rugulose; behind the eyes is a broad cream-coloured stripe, which extends to the base of the mandibles. The thorax rugose, with large punctures on the metathorax; the anterior and intermediate legs ferruginous. Abdomen: the first segment, which forms the petiole, transversely striated; the rest of the abdomen smooth and shining; the ovipositor more than one-third longer than the body; the wings hyaline, the nervures black."

This species is from Waigiou Island, near New Guinea. It appears to show affinities with *D. salomonis* Westw. and *P. pictipes* Roman, both from the same region, but the details are too scant to place it with certainty.

#### MEGISCHUS TARSALIS Smith.

*Megischus tarsalis* Smith, Journ. Proc. Linn. Soc. Lond. v. p. 137 (1861), ♀.

"*M. niger*, pedibus anticis et intermediis ferrugineis, tarsis posterioribus rubris, alis subhyalinis.

"*Female*. Length 9 lines. Black; the head coarsely sculpturated, on the face transversely so; the front with a transverse ridge, before which are two acute tubercles touching the eyes, and a central, more elevated one, a little in advance. The thorax coarsely punctured, the prothorax forming an elongated neck; the anterior and intermediate legs ferruginous; the dilated apical portion of the posterior tibiæ and the tarsi bright ferruginous; the posterior coxæ rugose, the femora bidentate; wings fuscous, the nervures dark brown. Abdomen: the ovipositor the length of the body; the basal segment or petiole finely striated transversely, the following segments smooth and shining; the ovipositor with a wide fascia of white a little before the apex. *Hab.* Bachian.

"This species differs from *M. coronator* in the form and situation of the tubercles on the front of the head; the neck is much longer and more slender; the ovipositor is as long as, but not longer than the body."

Schletterer tentatively synonymizes this species with *S. tarsatus* Sichel, with which it corresponds in the infumation of the wings, length and colour of terebra, sculpture of petiole, and, to some extent, in the sculpture of head and thorax. It differs in having the head black, thorax coarsely punctate, and in the much smaller size. The details given are insufficient for certain identification.

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## EXHIBITIONS AND NOTICES.

May 9th, 1922.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

The SECRETARY exhibited, and made remarks upon, a medal struck to commemorate the 150th Anniversary of the Royal Academy of Belgium.

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Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, a series of cinematograph-films illustrating various stages in the life-history of the Wood-Ant (*Formica rufa*) and of the Common Wasp (*Vespa germanica*), and asked the Society to accept the series for its Zoological Film Library.

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Dr. CHAS. F. SONNTAG, F.Z.S., exhibited, and made remarks upon, a series of specimens and lantern-slides illustrating some points in the Anatomy and Physiology of Whales.

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May 23rd, 1922.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of April, 1922:—

The registered additions to the Society's Menagerie during the month of April were 369 in number. Of these 95 were acquired by presentation, 105 were deposited, 156 were purchased, 3 were received in exchange, and 10 were born in the Menagerie.

The following may be specially mentioned:—

A pair of Abbott's Duikers (*Cephalophus spadix*), new to the Collection, from Usambara, presented by H.E. Sir Horace Byatt on April 1st.

1 Gambian Pouched Rat (*Cricetomys gambianus*), from French West Africa, presented by Curtis G. Lampson, Esq., on April 3rd.

1 King Guereza (*Colobus polycomus*), from West Africa, deposited on April 28th.

2 Vociferous Sea-Eagles (*Haliaëtus vocifer*) and 2 Tufted Umbres (*Scopus umbretta*), from Tanganyika Territory, presented by H.E. Sir Horace A. Byatt, K.C.M.G., on April 1st.

2 Tufted Umbres (*Scopus umbretta*), presented by Mr. J. D. Loveridge, F.Z.S., on April 1st.

2 Australian Cat-birds (*Elurædus viridis*), from New South Wales, new to the Collection, purchased on April 21st.

6 Laughing Kingfishers (*Dacelo gigantea*), from South Australia, purchased on April 13th.

4 Kagus (*Rhinocetus jubatus*), from New Caledonia, purchased on April 21st.

2 Tawny Frogmouths (*Podargus strigoides*) and 5 Regent Birds (*Seleucidés chrysocephalus*), purchased on April 21st.

Mr. R. I. POCKOCK, F.R.S., F.Z.S., exhibited, and made remarks upon, a living example of the rare Bush-Dog *Speothos venaticus*.

Mr. E. G. BOULENGER, F.Z.S., and Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, a cinematograph record which they had taken illustrating the life-history of the Axolotl (*Amblystoma tigrinum*).

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, a series of photographs he had taken of some recent important additions to the Society's collection of Birds.

The Rev. H. N. HUTCHINSON, M.A., F.Z.S., exhibited, and made remarks upon, a plaster cast of a model reconstruction of the marine reptile *Peloneustes philarchus*, a Pliosaur from the Oxford Clay, stating that he had received valuable assistance from Mr. Ed. Godwin in completing the model.

### June 13th, 1922.

Prof. E. W. MACBRIDE, D.Sc., LL.D., F.R.S., Vice-President, in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of May, 1922:—

The registered additions to the Society's Menagerie during the month of May were 489 in number. Of these 336 were acquired by presentation, 14 were deposited, 122 were purchased, 4 were received in exchange, and 13 were born in the Menagerie.

The following may be specially mentioned:—

1 Bush-Dog (*Speothos venaticus*), from Northern Brazil, presented by H. J. Lynch, Esq., on May 23rd.

1 Californian Sea-Lion (*Otaria californica*), born in the Menagerie on May 27th.

2 European Beavers (*Castor fiber*), from the River Nidelven, Norway, purchased on May 23rd.

A collection of birds from Colombia, presented by Mr. W. K. Pomeroy, F.Z.S., on May 6th, including 2 Colombian Red-rumped Hangnests (*Cassicus uropygialis*), new to the Collection; 2 Crimson-backed Tanagers (*Rhamphocelus dimidiatus*); 4 Colombian Crested Colins (*Eupsychortyx leucopogon*), and others.

1 Selater's Curassow (*Crax selateri*), 1 Crested Curassow (*Crax alector*), and 2 Purplish Guans (*Penelope purpurascens*), from Brazil, presented by Dr. Paulo de Silva Prado on May 12th.

3 Leadbeater's Cockatoos (*Cacatua leadbeateri*), hatched in the Menagerie on May 19th.

1 Shovel-footed Ceratophrys (*Ceratophrys cultripes*), from Morro Velho, Brazil, new to the Collection, presented by George Chalmers, C.M.Z.S., on May 29th.

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The SECRETARY briefly described the technical side of the Council's scheme to establish an Aquarium in the Society's Gardens.





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## NOTICE.

The 'Proceedings' for the year are issued in *four* parts, paged consecutively, so that the complete reference is now P. Z. S. 1922, p. . . . The Distribution is usually as follows:—

Part	I.	issued in March.
"	II.	" June.
"	III.	" September.
"	IV.	" December.

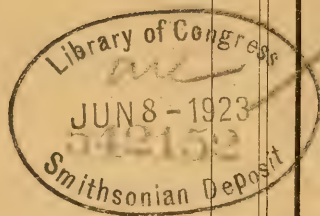
'Proceedings,' 1922, Part II. (pp. 205-481), was published on June 28th, 1922.

The Abstracts of the 'Proceedings,' Nos. 229-231, are contained in this Part.

The dates of Publication of 'Proceedings' 1830-1858 will be found in the 'Proceedings' for 1893, page 436.

The dates of Publication of 'Transactions' 1833-1869 will be found in the 'Proceedings' for 1913, page 814.

PROCEEDINGS  
OF THE  
GENERAL MEETINGS FOR SCIENTIFIC BUSINESS  
OF THE  
ZOOLOGICAL SOCIETY  
OF LONDON.  
1922.



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PART IV.  
CONTAINING PAGES 837 TO 1276, WITH 13 PLATES AND  
145 TEXT-FIGURES.

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37. Notes on East African Birds (chiefly nesting habits and stomach contents) collected 1915-1919. By ARTHUR LOVERIDGE, F.E.S., C.M.Z.S.

[Received October 22, 1922 : Read November 21, 1922.]

The following notes are based on a collection of about a thousand skins representing 51 families, 216 genera, and 402 distinct species, besides several hundred eggs; it does not include a collection made in Uganda, but refers to those from the coastal colonies—Kenya Colony (then B.E.A.); Tanganyika Territory (then G.E.A.); Portuguese East Africa; Natal.

No object would be served in publishing the whole list of species, and the following field-notes selected from my diary relate to the nesting habits, stomach contents, European migrants, and other items of general interest.

The principal localities mentioned in the following pages are:—

*Kenya Colony*.—Bissel, Fort Hall, Frere Town, Kabete, Kedong Valley, Kijabe, Lake Naivasha, Nairobi, Voi.

*Tanganyika Territory*.—Dar-es-Salaam, Dodoma, Kongwa, Longido West, Makindu (Msiha River), Morogoro, Mpwapa, Mt. Meru, Ngari Mtoni, Soko Nassai, Tabora, Uluguru Mts.

*Portuguese East Africa*.—Lorenzo Marques, Lumbo (mainland opposite Mozambique).

*Natal*.—Durban.

I should like to take this opportunity of thanking Dr. V. G. L. van Someren, Dr. Hartert, and Mr. Arthur Goodson for undertaking the identification of many of the specimens. To Dr. Hartert, I am also indebted for his kindness in correcting proofs and seeing these notes through the press.

Some half-dozen new species or races contained in the collection have been described by Dr. van Someren.

NECTARINIA REICHENOWI Fisch.

This Sun-bird is particularly associated in my mind with the red inflorescences of *Leonitis leonurus*, of which it is particularly fond. Clinging to the stem of one of these plants, the bird rapidly runs around the circlet of red flowerlets, in quick succession driving its beak into the tube-like bases of the flowers and passing on to the next till that particular plant is exhausted (Kijabe, 26. vi. 15).

CHALCOMITRA SENEGALENSIS INÆSTIMATA Hartert.

The species has a very wide distribution in East Africa, having been met with in strikingly different types of country. In captivity it does well on sugar slightly moistened; to this I added



a few ants, for without such additional insect diet they do not thrive for long. It was a surprise how quickly the bird took to this form of food, sitting on the edge of the bowl and sipping at the mixture, with occasional intervals in which it gave vent to the characteristic whistling chirp. I have seen the Scarlet-breasted Sun-bird hovering in the air and taking termites on the wing (Morogoro, 10. iv. 18).

Nest with one egg (Morogoro, 19. ii. 17); nest with two eggs (Morogoro, 13. iii. 17); building (Morogoro, 9. xii. 17).

*CHALCOMITLA VERREAUXI* A. Sm.

Verreaux's Sun-bird was found nesting on the Bluff at Durban (21. xii. 14); the two eggs were of a chocolate colour.

*ANTHREPTES COLLARIS* Vieill.

The Natal Collared Sun-bird also found nesting on the Bluff with two eggs (Durban, 21. xii. 14).

*MOTACILLA VIDUA* Sundev.

The East African Pied Wagtail is one of the sweetest songsters in the country, and quite rivals a canary. Its favourite perch when singing appears to be the ridge of a roof; in such a situation I have seen three or four of these wagtails in company with a row of swallows (Morogoro, 14. ii. 17).

A nest containing three hard-set eggs was found on the brink of a waterfall at Kabete—such a waterfall and surrounding scenery as one might find in the Vale of Neath (Kabete, 26. v. 15).

*MOTACILLA FLAVA CAMPESTRIS* Pall. (*cf.* Ibis, 1921, p. 666).

During the month of November 1918 large flocks of Yellow Wagtails were to be met with at Dar-es-Salaam. They were particularly plentiful on the land near the sea-front, where they ran at the heels of the transport oxen which were pastured there.

*MACRONYX CROCEUS* Vieill.

A nest of the Yellow-breasted Pipit containing a single egg which disappeared the following day (Nairobi, vii. 15).

*SERINUS STRIOLATA AFFINIS* Richmond.

Nest with three eggs (Kabete, 24. v. 15).

*PASSER GRISEUS SWAHILICUS* Neum.

A nest of the Swahili Grey Sparrow containing three eggs in the masonry of a house. Both nest, eggs, and situation similar to those of the English Sparrow (Kongwa, 25. iv. 17).

*HYPOCHERA ORIENTALIS* Reichw.

Found a freshly-killed male lying dead in the bush without any visible signs of violence; one leg was missing from the knee,

but this was evidently an old injury, as it had long since healed. Whilst examining it, my attention was attracted by the demonstrations of a Shrike (*Harpolestes senegalensis orientalis*), and a short search discovered its nest with the hen bird sitting on the clutch. Was it possible that the Shrike had killed the Weaver, which had been unable to escape owing to its crippled condition? (Morogoro, 29. iii. 17).

*COLIUSPASSER ARDENS TROPICUS* Reichw.

Nests of the Red-collared Whydah with three eggs in each were found on 9. iv. 17 and 1. vi. 17, and many more between those dates, the species being quite common at Morogoro (Morogoro, 1917).

*COLIUSPASSER LATICAUDA* Licht.

Many nests were found on the plains at Nairobi between 22. v. 15 and 5. vi. 15, containing three eggs, which comprises the clutch. Two clutches of three eggs were found at the same place on 7. v. 19. (Nairobi).

*COLIUSPASSER EQUUS* Hartl.

Four nests with two eggs in each were found between 13 & 23. iii. 17. It would appear that two is often the full clutch. The nest is similar to those of other members of the genus. At first a framework in the shape of an oval is made between two or more stout grasses at a height of 3 feet from the ground, or thereabouts. A loosely-built domed grass net is woven on to the framework, and the eggs laid in the bottom of the nest without lining of any kind (Morogoro, 1917).

*COLIUSPASSER JACKSONI* Sharpe.

The males of Jackson's Whydah and the foregoing species dance round and round the female as she sits on a tuft of grass, the object of the dance being to display the extraordinary long black tail-feathers which are put on for the breeding season. The dance is really a hop, and it is quite ridiculous to see the birds appearing and disappearing as if shot into the air by some unseen spring. Round and round goes the bird, till the grass is trodden down in the vicinity of the central tuft to such an extent that one could hardly credit that it was the work of so small a creature. Doubtless they resort to the same spot day after day. The dancing rings, about two feet in diameter, are common enough, and become almost bare of grass. The lengthy tail seems to hamper the bird in flight as it leaves the grass or bushes; occasionally one is seen with its tail at right angles to its body as it sits on a branch or briar. Unwieldy as they appear, attempt to catch one, and you always find you just fail; at the eleventh hour the owner of the tail manages to get under way (Nairobi, 1. v. 9).

*PYROMELANA XANTHOMELANA* Rüpp.

Nesting in company with *P. nigroventris* and *P. flammiceps*. Nests containing three eggs each found on 20.iii.17 and 5.iv.17 (Morogoro, 5.iv.17).

*PYROMELANA NIGRIVENTRIS* Cass.

Nests of the Black-bellied Bishop-bird with full clutches of three eggs were found from 14.ii.17 to 30.iii.17. So common were these nests in places, that as many as thirty could be found in about the same number of square yards. The most favoured locality where I met with them was on the edge of a belt of dense thorn-bush scrub at Morogoro. Sharp spear-grass mingled with other kinds grew rank to one's shoulders, whilst scattered thorn-bushes obscured by the luxuriant vegetation waited to entangle the feet of the unwary. Several species of Yellow Weavers flew about in the trees from which their pendent nests were hung; below were the agitated Bishop-birds, whose scarlet-and-black plumage showed to best advantage against the rich green of the freshly-grown grass. Many other birds frequented the spot, and joined their voices to the tumult which greeted the intruder. The nests of the Bishop-birds were so similar to those of the *Coliuspasser* just described that a fresh description is unnecessary (Morogoro, 14.ii.17).

On one occasion (20.ii.17) when visiting this spot, I found a dead female Black-vented Bishop-bird sitting upon three eggs containing live young! A few ants were crawling about the eyes and mouth of the dead bird, but it was so fresh that I was able to leave it twenty-four hours before skinning. Seventeen days later I examined the same nest and found two more eggs in it (9.iii.17), so it appeared as if the male had installed another mate in the nest. The death of the bird may also be explained by the presence of a Green Mamba (*Dendraspis angusticeps*), which was lying sunning itself on a thorn-bush not 20 feet away. It is possible to suppose that it had bitten the bird, which was just able to flutter back to its home before succumbing to the effects of the poison (Morogoro, 9.iii.17).

*PYROMELANA FLAMMICEPS* Swains.

The eggs of the Fire-crowned Bishop-bird are the same hedge-sparrow-egg blue as the preceding species, but are readily distinguishable by their slightly larger size. Nests containing full clutches of three eggs were found between 23.iii.17 and 5.iv.17 (Morogoro).

*QUELEA INTERMEDIA* Reichw.

Nest with three eggs (Nairobi Plains, 7.v.19).

*QUELEA CARDINALIS* Hartl.

Four nests of the Cardinal Finch containing three eggs each were found (Nairobi, 7 & 8.v.19).

SPERMESTES sp., either CUCULLATA Swains. or SCUTATA Heugl.

Green-headed Mannikin. Two and four eggs respectively (Kabete, 24. v. 15); two eggs (Soko Nassai, 22. v. 16); one egg (Morogoro, 30. iv. 17); two eggs (Nairobi, 7. v. 19).

I have frequently found the hen-birds sitting on their eggs in the deserted nests of other species of Weaver, which they do to save themselves the trouble of building. A nest was situated in a very exposed thorn-bush on an exposed hillside at Kabete. Two of the eggs were perfectly fresh and two were perfectly bad, so much so that they exploded when pricked with a pin; the fifth egg was empty, with a very small hole in its side such as might have been made by a bird's claw, and the contents removed by ants. Another of these weaver-finches was sitting on its eggs in the nest of a weaver (*Ploceus xanthops*?) which had been built in sedges growing in the waters of a swamp at Soko Nassai; yet another had adopted the retort-shaped nest of another species of *Ploceus*, which was situated in a banana-palm, about 10 feet from the ground, growing on the banks of the river at Morogoro.

URÆGINTHUS BENGALUS ANGOLENSIS Linn.

One egg of the Blue-breasted Waxbill in a nest (Lumbo, 28. x. 18).

URÆGINTHUS NIASSENSIS Reichw. Niassa-land Bengali.

On the outward voyage to East Africa, when at Lorenzo Marques, I made a note in my diary that a small blue bird had built its nest in a thorn-bush just above that of a wasp, and speculated whether it had been done for protection. I forgot the incident entirely until indexing my notes three years later. The species was probably *U. b. angolensis*. Two years later, at Morogoro, I found many nests of *U. niassensis*. In nineteen cases out of twenty these were built over the paper nests of wasps, so that one could not approach one's hand through the thorns before the wasps began to threaten and fly round. I watched a pair of these birds building over a wasp's nest, and so am certain that it is not the wasps which build beneath the bird's nest for the sake of shelter from the rain, though doubtless the arrangement is mutually beneficial. At Mombasa, I have seen the same thing with *U. b. brunneigularis*, but at Nairobi, where one of these charming little blue weavers is very common, I never recollect having seen its nest above a wasp's. The same at Lumbo, where *U. b. angolensis* was very abundant and its old nests were to be seen in almost every thorn-bush.

I was very interested in coming across this paragraph in Belt's 'The Naturalist in Nicaragua.' "A yellow and brown flycatcher builds its nest in these bushes, and generally places it alongside that of a banded wasp, so that with the prickles and the wasps it is well guarded" (p. 222).

Five, four, and two eggs were found in three nests on 13. iii. 17, and three eggs in a nest on 30. iii. 17 (Morogoro)



*LAGONOSTICTA SENEGALA*, subsp. n.

The birds exhibit a preference for the thatch of grass huts for a nesting-site, and make themselves perfectly at home, paying but little attention to the human occupants of the place; in one such case the favourite perch was the towel-rail. This nest contained three eggs and a parasitic egg slightly larger; the male bird was sitting on the lot (Morogoro, 21. vi. 17). Another nest was found to contain four eggs on 30. iii. 17.

These charming little birds, which may often be seen in company with the blue *Uræginthus* hopping about on paths at one's very feet, have been rather aptly christened "Animated Plums" by Sir Frederick Jackson, on account of the rosy or plum colour of the males of most of the species. Just before writing up these notes, I was watching a pair sitting side by side on the bough of a fir-like tree; they had sidled up to one another till they could get no closer. The hen was preening the head plumage of the male, and afterwards touched beaks, making as pretty a little group as one might wish to see.

*PYTELIA MELBA KIRKI* Shelley.

Found a nest with three pure white eggs in a very low bush. The nest was very similar to that of *Uræginthus*, being built of flowering grass heads loosely put together, with a tubular entrance in one side (Morogoro, 9. iv. 17). The species is often to be found hopping about after dusk, feeding long after other birds have gone to roost for the night (Morogoro, 23. vii. 17).

*AMBLYOSPIZA UNICOLOR* Fisch.

Builds a finely-woven nest attached to reed-stems over water; such a nest containing three eggs was found (Morogoro, 20. iii. 17).

*PLOCEUS REICHENOWI* Fisch.

Clutches consist of two or three eggs; several such were found between 20. v. 15 and 20. vi. 19. One of these birds fell from a tree just as an acquaintance of mine was passing beneath. It was still warm when brought to me and not a feather disarranged. The only signs of violence were blood oozing from the nostrils and the beak full of clotted blood. On skinning, I found extensive hæmorrhage around the eyes and ears, in intestines, lungs, and about the heart. It appeared to me to have died from the poison of a venomous snake, probably the Boomslange (*D. typus*) (Nairobi, 18. ix. 19).

*PLOCEUS NIGRICEPS* Layard.

Some scores of nests of the Black-headed Weaver were examined at Morogoro between 13. iii. 17 and 11. iv. 17, and found to contain pure white eggs, white eggs with red blotches, pure blue eggs, and blue eggs with red blotches; the usual number for a clutch appeared to be two; three, however, was not uncommon. A bird which I took to be this species was engaged in stripping the leaves of a Bussu Palm into threads. It



accomplished this by flying to a frayed edge and taking this in its beak, flying slowly down with it (Morogoro, 20. xii. 16).

One of the Black-headed Weavers surprised me to-day by dodging after a Praying Mantis in the manner of a flycatcher. Almost immediately after catching the insect, however, it dropped it; presumably owing to the mantis making good use of its fore-legs (Morogoro, 7. xii. 17).

#### PLOCEUS SPEKEI Heugl.

Out of a large colony of freshly-made nests found on the plains and dependant from a thorn-tree, only one was found to contain anything, and that but a single fresh egg (Nairobi, 10. vii. 15).

#### ORIOLES BRACHYRHYNCHUS LÆTIORE Sharpe.

The note of the Black-headed Oriole is as lovely as its plumage. On a hot afternoon, when all is still, you may be surprised by suddenly hearing a liquid cry of "tokio" ringing out very clearly quite close to you. You look in the direction from which the sound came and hear it again, but perhaps behind you. The bird appears to be aware that its cry is likely to draw attention to it, and so frequently after giving a call it slips away to some fresh perch, where it is concealed by the foliage. The natives say that it calls "ndugu, ndugu," which is Kiswahili for "brother, brother." By imitating the call, I have frequently been successful in attracting the bird to the very tree beneath which I was waiting (Morogoro, 7. vii. 17).

#### AMYDRUS MORIO RÜPPELLI Verr.

Rüppell's Red-winged Starling and *A. tenuirostris* go about in the same flocks, for both species fell to one shot from a gun when they were pillaging fruit-trees in the Uluguru Mts. *A. walleri* was taken later near the same place. A solitary bird was shot on the lower slopes of the mountain near Morogoro, where they very rarely come; its neck was stripped bare of feathers, which gave it so peculiar an aspect that I quite failed to recognise it till shot. The only explanation I could think of was that it had been snared at some time or had been worried by lice and scratched them off; the skin was, however, uninjured. At Fort Hall, *A. m. rüppelli* made such a noise on the roofs and gutters of the houses that it was a perfect nuisance; they seemed to have adapted themselves to the habitations of man as much as the English Starling.

#### SPREO SUPERBUS Rüpp.

The White-banded Glossy Starling will build in holes in cliffs or trees, or make a great untidy nest in thorn-bushes. A pair were seen carrying food to their chirping young in a cliff-fissure in the Kedong Valley (vii. 15). A nest containing young was found in a hollow tree at Longido West (30. i. 16). Another nest with young was found in a thorn-tree at Dodoma (20. xii. 18), whilst nests with bright blue eggs were found at Mpwapwa (30. iv. 17).

*CORVUS SCAPULATUS* Daud.

Pied Crow. At Lumbo, I found a broken egg-shell in a cultivated patch, and on enquiry found that the native proprietor had pulled the nest down from a cocoanut palm; after this I searched and found a good many nests, one containing three very large young ones and another some newly-hatched (Lumbo, x. 18).

*DICRURUS AFER LUGUBRIS* Rüpp.

At Government Farm a White-shouldered Crow was giving vocal expression to its feelings after the manner of its kind, cawing hoarsely in the midst of a field of stubble. From a nearby mango-tree, stooping like a hawk, came a Black Drongo, and went straight for the croaker, who took to wing at the last moment. Its more active assailant landed on its back when about 40 feet from the ground and gave the Crow a good pecking, then, clearing off, it returned triumphantly to its perch. I searched for, but found no signs of a nest; possibly the Drongo had an ear for music and disapproved of the raucous cries (Morogoro, 20. xii. 16).

*LANIUS COLLARIS HUMERALIS* Stanley.

This Shrike, which is very common at Nairobi, breeds all the year round, for at any season the young birds may be seen on the telegraph wires clamouring for food with shivering wings. Nests with eggs were found on the following dates:—One (13. i. 15); two (22. v. 15); four (1. vi. 15); three (5. vi. 15). Nearly all the nests were built in thorn-trees. There is no lack of thorns for their larders, and grasshoppers appear to be the most common food; huge caterpillars were also found, whilst on one occasion a small frog (*Rappia* sp.) was found impaled on the point of an aloe. A friend told me that he once found a small blue weaver (*Uraginthus* sp.) impaled on a thorn and still alive. With diabolical ingenuity the Shrike had twisted other thorns across in front to prevent the bird freeing itself (Nairobi, 1. vi. 15).

*LANIARIUS SUBLACTEUS* Cass.

A nest of the Lesser Pied Shrike with one egg (Lumbo, 28. x. 18).

*HARPOLESTES SENEGALA ORIENTALIS* Cab.

The Greater Red-winged Bush-Shrike was found nesting on the 26th and 29th of March, 1917. In both instances only two eggs were laid. The nests were very shallow, composed of a base of small twigs and rootlets with a lining of much finer roots. They were both in bushes, one being at a height of 4, the other 5, feet from the ground (Morogoro, 29. iii. 17). Nest with young about 7 feet from the ground (Morogoro, 4. iv. 17).

*MALACONOTUS POLIOCEPHALUS BLANCHOTI* Steph.

Chestnut-breasted Thick-billed Shrike. One of these beautiful Shrikes was seen sitting on its nest in the fork of a rubber sapling which had sprung from the stump of a felled rubber-tree. The nest was at a height of 18 feet from the ground, and was slightly hidden by a few withered yellow leaves, but all the surrounding trees in the plantation were bare of foliage. The eggs, of which there were three in the nest, were slightly larger than an English Blackbird's, and were thickly freckled with brown and faint purple on a white ground. One contained a chirping chick, already breaking from its shell, and this I left; the other two were unfertile and easily blown (Morogoro, 2. xi. 17).

*EUROCEPHALUS RÜPPELLI* Reichw.

The White-headed Shrike was found building a very beautiful and solid nest on the tip of a branch of mimosa-thorn quite 12 feet from the trunk and perhaps 9 feet from the ground (Kongwa, 25. iv. 17).

*CRATEROPUS KIRKI* Sharpe.

A nest of this species was taken on a mimosa bough about 10 feet from the ground. It held three eggs of Kirk's Babbling Thrush and one slightly larger egg of a Cuckoo (*Coccyzus cafer*); all the eggs were uniform greenish-blue (Lumbo, 22. x. 18). A cock-bird was found sitting on three eggs (Morogoro, 23. iii. 17).

*PYCNONOTUS BARBATUS MICRUS* Oberhols.

The Yellow-vented Bulbul breeds during the greater and lesser rains, if not all the year round. Many nests were found at Morogoro on the following dates:—Two young ones in a nest in boughs of a flamboyant (8. xii. 17); two eggs and three eggs in a similar situation (14. xii. 17); young in a nest in a bunch of bananas in palm (16. i. 18); two eggs (26. iii. 17); and one egg (11. iv. 17).

After a night of heavy rain, I witnessed a somewhat unusual sight. Not 15 yards from where I was standing, termites were flying from their nest-holes. No less than seven species of birds were engaged in catching them, of which five were seed or fruit eaters. The birds were two Weavers (*Lagonosticta senegalensis* subsp.), two Waxbills (*U. niassensis*), one Finch (*S. icterus barbatus*), one Sparrow (*P. g. suahelicus*), two Pied Wagtails (*M. vidua*), and two of these Bulbuls, whilst, to add to the colour-effect, a dainty Scarlet-breasted Sun-bird (*C. s. inæstimata*) hovered above and captured the termites on the wing (Morogoro, 10. iv. 18).

*PYCNONOTUS TRICOLOR PALLIDUS* Roberts.

Very abundant at Lumbo. Five nests, each containing two eggs, were found on 28. x. 18.

*ANDROPADUS INSULARIS* Hartl.

Many nests of the Coast Olive Bulbul were also found, and five clutches of two eggs each taken; two would appear to be the normal number for a clutch. The eggs are white, scribbled and blotched with brown and faint purple at the larger pole, in some cases all over. The nest is small and shallow, composed of twigs, and lined with fine rootlets (Lumbo, 28. x. 18).

*PRINIA MYSTACEA TENELLA* Fisch.

Nests of the White-eyebrowed Grass-Warbler, with three eggs in each, were found on 22.iii.17, 5.iv.17, and 21.vi.17 at Morogoro.

*SYLVIETTA WHYTEI* Shelley.

This Warbler constructs a most beautiful purse-like nest, which it hangs from the branches of a thorn-bush. Three nests with eggs were found at Lumbo on 28.x.18, and a bird was sitting on two eggs at Morogoro on 28.xi.18. Two appears to be the normal clutch.

*CISTICOLA LUGUBRIS* Rüpp.

A deserted nest of the Brown-headed Grass-Warbler, containing one egg, was found; from the interior roof of the nest depended the paper nest of a wasp, whilst a small company of solitary bees had their comb in the bottom (Ruaraka River, nr. Nairobi, 11. x. 19).

*CISTICOLA ERYTHROPS* Hartl.

A nest of the Rufous-fronted Grass-Warbler containing three eggs (Nairobi, 5. vi. 15).

*CICHLADUSA GUTTATA* Heugl.

The Spotted-crested Ground-Thrush is a very sweet singer, generally holding forth from thickets just before sunset; it does not expose itself when singing. The mud nest is built upon a branch or, more rarely, in a fork; it is very deep. The eggs are of a uniform blue colour. A broken egg beneath a nest on 12. i. 17; in another nest young on 22. ii. 17; two eggs in a nest found on 4. iv. 17 and two more in one on 6. iv. 17 (Morogoro, 1917).

*TCHITREA CRISTATA SUAHELICA* Reichw.

I have seen this Paradise Flycatcher hovering up the trunk of a tree, picking the insects off the bark whilst on the wing. It constructs a beautiful cup-shaped nest, which it covers with lichen; one such was attached to some epiphytes at a height of 8 feet above a mountain torrent, and contained young (Uluguru Mts., 28. xi. 18).



*RIPARIA RUIFIGULA* Fisch.

Nest of the Rufous-throated Rock-Martin, containing three eggs, attached to the wall of a cattle-shed (Kabete, 6. v. 18).

*HIRUNDO SMITHI* Leach.

A nest of the Wire-tailed Swallow with three eggs (Morogoro, 23. vii. 17); with two eggs and apparently deserted (Frere Town, 1. vii. 19). At Morogoro on 14. ii. 17, I made a note that thousands of swallows had been gathering on the telegraph wires for the past few days, apparently for migration.

*HIRUNDO PUELLA UNITATIS* Scl.

The Smaller Stripe-breasted Swallow was associated with the preceding species in the assemblage for migration at Morogoro (14. ii. 17). A dead bird was found upon her nest, which contained three eggs, one of which was plain white (Kongwa, 25. iv. 17).

Along the river these birds nested against the rocks, but almost every house in Morogoro had its nest with the typical long entrance passage of mud. The birds are most persistent, and will continue to build in rooms, where they are not welcome and where their nests are knocked down again and again. The earliest date at which I found a nest at Morogoro was on 25. vi. 17, and the latest 15. viii. 17. Three eggs is the invariable clutch.

On 23. vii. 17, I found a nest with no entrance tunnels, and broke a small hole into it, but found no eggs. On again examining it a few days later, there were three eggs, and the hole I had made had been neatly finished off with mud to form a window or third outlet. In one instance I opened a nest carefully, and found three eggs; two were white with faint reddish speckles and the third pure white (23. vii. 17); these I took. On 1. viii. 17, I again visited the nest; the small hole I had made had been repaired, and three eggs again laid of which one only was white. On 15. viii. 17 a third visit was made, and again three eggs found of which one was white. A fortnight later the hole had been again repaired, and the bird was sitting. I did not molest her further, as such persistence deserved its reward, and it was the variation in the clutches that caused me to rob her.

Calling on an English sergeant on one occasion, I found him nursing one of these swallows, which had a broken wing; he was endeavouring to feed it on crumbs and meal. He had, it transpired, thrown a stone at the bird as it sat chirping on the roof-ridge: to his surprise and grief he hit it, and was now endeavouring to restore it to health by a vegetarian diet!! (Morogoro, 27. i. 17).

*HIRUNDO EMINI* Reichw.

Emin's Swallow was only once met with at Morogoro (31. vii. 17) when evidently on migration, three birds in poor plumage being seen. A pair of these birds, after starting the foundations of twenty-one nests on the roof-rafters of my office verandah,



appear to have at last selected a spot exactly above the most frequented place—*i. e.*, between the stairs and door (Nairobi, 8. vi. 19).

15. vi. 19. The birds sat with dabs of mud in their beaks, uttering their peculiarly sweet metallic notes. The nest is about finished.

22. vi. 19. During the week the entrance tunnel has been under construction, the work proceeding very slowly.

28. vi. 19. The birds appear to have gone away.

1. viii. 19. The weather has been very cold and dull during the past month, and the swallows have only twice put in an appearance, when they added a few feathers to the nest.

7. viii. 19. Felt in the nest, and there appeared to be no lining worth mentioning.

14. viii. 19. Nest with lining of grass and feathers, and one broken egg *with a streak of red* in it, lying on the ground, having been pulled down by a ruthless native. When did the egg get incubated? Is it possible I did not feel to the bottom of the nest on the 7th inst.?

#### CYPSELUS AFFINIS Hardw.

The Indian Swift is extraordinarily abundant at Frere Town, where great numbers of them fly about, screaming, towards evening; in fewer numbers they are to be seen at most hours of the day. They build along the cliffs or under the eaves of verandahs. The nests are constructed of feathers and straw, so cemented together with mucilage that they have the strength and consistency of cardboard. A large number of nests were examined on 1. vii. 19; ten of these held young, three held incubated eggs whose clutches numbered four, four, and three respectively. One nest had a single fresh egg in it.

A nestling was picked up at Morogoro, 29. x. 17.

#### TACHORNIS PARVUS Verr.

My notes on the curious nesting habits of the Lesser Palm-Swift have already been published\*. On July 17th, 1917, I revisited the colony which were nesting in the cocoanut-palms (not banana-palms, which was printed in error). One nest was completely upside down, having been built that way; the bird was brooding two eggs which were nearly ready to hatch. Another nest had a bad egg which had a small hole in the top of it, probably made by a bird's claw. Another held newly-hatched young; yet another was occupied by downy young. In one instance both birds were on the nest and appeared to be paired. Some nests were unfinished, possibly abandoned.

On 4. ii. 18, I again visited the spot; in one nest there were two fresh eggs, several hard-sat clutches in others, newly-hatched and half-grown young in the rest.

\* "Observations on the Nesting Habits of the Palm Swift etc." Mem. Proc. of the Manchester Lit. & Phil. Soc. vol. lxi. pt. ii. (1919).

*CAPRIMULGUS EUROPÆUS* Linn.

The European Nightjar was collected at Morogoro (24. ix. 17).

*CAPRIMULGUS FOSSEI MOSSAMBICUS* Hartl.

A single egg, perfectly fresh, was picked up and brought to me by a native. A good series of birds were collected (Lumbo, 28. x. 18).

*CORACIAS GARRULUS* Linn.

The European Roller on migration was met with on several occasions. An immature female was shot at Nairobi (29. x. 15). Large numbers of them were seen at Longido West (ii. 16). Specimens were obtained from a flock at Morogoro (10. xii. 17).

*CORACIAS CAUDATUS* Linn.

The Lilac-breasted Roller was seen clinging to a blasted tree just below a suitable nesting-hole. On both occasions when I approached the tree I was made the subject of very noisy demonstrations, so I concluded that they were nesting in the hole (Bissel, 20. xii. 15).

A pair of birds were obtained at Kongwa (23. iv. 17) in very fine plumage, and during that year they were extraordinarily abundant at Morogoro. In the stomachs of several specimens were found many nauseous and warningly coloured grasshoppers (*Zonocerus elegans* Thunb.).

Some three pairs lived in the neighbourhood of the camp at Lumbo. One pair frequented a large baobab-tree, which served as a jumping-off ground for their little excursions to rag the soberly-garbed crows, which they chivvied mercilessly about. After these little excursions, one or both of them would soar higher and higher above their favourite tree, and then come tumbling down in the most extraordinary way, more like a winged bird that is making an effort to recover itself than a healthy one. Towards October 1918, I saw one of the birds outside a hole near the top of the baobab, but thought climbing out of the question. At the end of the month a native brought me a Roller, which he told me he had caught on its nest in a hole in a tree; it was sitting upon two eggs which he had broken. I refused to purchase the bird, but from the information that he gave me I concluded that it was from this baobab that he obtained it, and, if so, this would explain their energy in driving off the crows. These birds were extremely shy of approach, whilst those met with at Morogoro were quite the reverse.

*MELITTOPHAGUS BULLOCKOIDES* Smith.

A colony of some fifty White-fronted Bee-eaters was found in an artificial pit some 20 cubic feet in size; the nesting-holes had been excavated in the sides of the pit (Ngari Mtoni, nr. Arusha, 17. iv. 16).

*MEROPS APIASTER* Linn.

A single pair, in very worn plumage, of the European Bee-eater were obtained at Morogoro (17. x. 17).

*LOPHOCEROS DECKENI* Cab.

A male and immature female Von der Decken's Hornbill were shot on 1. vi. 17 at Morogoro. The male had two large complete mantids in its stomach, whilst the female had only beetles. The young female was strikingly different from the male. Its bill was black instead of orange-red and yellow; the wings were also spotted with white.

*LOPHOCEROS MELANOLEUCUS SUAHELICUS* Neum.

The Swahili Crowned Hornbill was common at Morogoro, the type-locality for the subspecies. I extract the following note from my diary under date 3. xi. 17 :—"The last few days we have had a small flock of these hornbills flying past in the morning and evening; apparently they return to the big trees along the river to roost. They usually frequent a group of trees quite close to my quarters for a short time before continuing their flight; one is soon made aware of their arrival by their shrill whistling cries. The birds do not sit together, but on separate branches, from which they make sudden and absurd dives as if they were top-heavy and could maintain their balance no longer. These little excursions are apparently after insects, though their stomachs more often contain the remains of fruit." And on 4. ii. 18 :—"One of these hornbills, which flew over the camp to-day, apparently had nesting (!) material in its beak."

Whilst out in the bush one evening, I came upon an open glade, thereby disturbing the most remarkable assemblage of typical African birds which I have ever met with in so small a compass. Some twenty Hoopoes (*U. africana*) rose, and perched for a few moments in the surrounding trees; a large red-billed Hornbill (*L. m. suahelicus*) sailed off in its own peculiar dipping flight. Wood-Hoopoes (*R. c. schalowi*) raised their noisy outcry. A red-headed Woodpecker (*C. scriptoricauda*) paused in its occupation of hammering a tree, caught sight of me, and dived off with a shrill whistle, so that the glade which was so full of life a moment before was left to myself (Morogoro, 14. vii. 17).

*LOPHOCEROS NEUMANNI* Reichw.

A female of Neumann's Hornbill, which was being noisily mobbed by a party of small birds whilst in flight, was found to have a praying mantis in its stomach (Morogoro, 28. xi. 17).

*ALCEDO SEMITORQUATA* Swains.

Half-collared Kingfisher. A native brought me two beautiful nestlings; their head, back, and wings were turquoise-blue, their breasts fawn-colour (Morogoro, 28. xi. 17).

*CORYTHORNIS CYANOSTIGMA* Rüpp.

Malachite Kingfisher. A nest of young ones was found in the river-bank at Morogoro (1917).

*HALCYON LEUCOCEPHALA* Vieill.

Brown-bellied Kingfisher. Having just stepped out of my tent to walk across to my grass-hut one morning, I heard a screech and a shrill whistling cry. There was a rush of small birds about me, and I was just in time to see a South African Lanner (*Falco biarmicus*) rise from its stoop with a kingfisher in its claws and speed away to a big tree some 20 yards off. I shot the Lanner promptly, and it fell stone-dead with the kingfisher in its claws (Morogoro, 17. i. 18).

*HALCYON CHELICUTI* Stanley.

Striped Kingfisher. Each morning as I wake I hear a pair of small kingfishers start shrilling—this coined word seems to describe the noise better than anything. The note is not unlike “peewit,” whistled through the top front teeth, but the one bird follows up its mate’s call, so that there is one continuous sound, and at first I thought it was one bird calling. As each in turn utters its note, it spreads its wings like a fan, then raises them above the level of its head, lowers and then closes them, repeating the performance constantly. It is a pretty spectacle to witness, as the wings and tail are partially pale blue and displayed to advantage. As these little kingfishers are no larger than sparrows, and select the topmost branches of the acacia-trees for their performance, it was some time before I could find out the perpetrators of the noise (Morogoro, 26. x. 17).

*HALCYON ALBIVENTRIS ORIENTALIS* Peters.

Oriental Brown-hooded Kingfisher. A young lizard (*Gerrhosaurus flavigularis*) was in the stomach of a specimen shot at Dar-es-Salaam, 26. vi. 18.

*COLIUS STRIATUS AFFINIS* Shelley.

Mouse-bird. I believe Dar-es-Salaam Colies are referable to this race, which was found nesting with three eggs on 1. ii. 19. A nest and three eggs were taken at Nairobi on 7. v. 19.

*COLIUS INDICUS PALLIDUS* Reichw.

Was collected at Lumbo, where there were many flocks in July and August; its cry was like that of a plover (*Stephanibyx*). After August they were only seen singly or in pairs; this should have put me on my guard, but it was not till I happened on a nest containing three eggs that it occurred to me that the birds had disbanded for breeding. Search being made, a dozen nests were found in October, but nearly all of them contained highly-incubated eggs or young. The eggs are round, dull stony-white



in colour, streaked, blotched, or freckled with reddish-brown in great variety. The nests were all situated in thorn-trees; those that were putting forth green shoots were given preference; they had deep foundations of thorny sprays, upon which was built a cosy nest of moss, lined with fine fibres or grass. The old birds sit very close, and make no attempt to leave if merely looked at; one's hand must be approached unreasonably close before they will slip off. The clutch was invariably three (Lumbo, 28. x. 18).

*SCHIZORHIS AFRICANA LEUCOGASTRA* Reichw.

Many species of Plantain-eaters were collected, but none were more difficult to obtain than this species, which frequents sandy thorn-bush country. At Dodoma its harsh cry was quite a feature of the scrub-life. The "ha-haa" (emphasis prolonged on second syllable) has quite a jeering sound as the bird rises from some conspicuous perch it has chosen on the top of a thorn-tree (commanding a good view of the dense thorn patch), and, flying off for a short distance, leaves the perspiring hunter to push his way through another few hundred yards of tangled undergrowth, with the probability of a recurrence of the flight, which seems always to be accompanied by the cry (Dodoma, 5. xii. 18).

*CENTROPUS MONACHUS* Rüpp.

A series of skins were obtained at Dar-es-Salaam and Lumbo. At the latter place the bird was very abundant, and was found to be feeding largely on maggots in the human faeces so common in the bush about the camp. The throat plumage in most of the skins was soiled with faecal matter, and a good deal was found in the stomachs of the birds along with the maggots. The offensive smell made the birds most unpleasant to skin. I watched a bird feeding in the early morning. The natives say that the skulking habits of this Cuckoo amongst the bushes are an evidence of its sense of shame for the diet which it has adopted (Lumbo, 21. vii. 18).

At the back of my tent was a large mango-tree whose base had been wired in to form a large circular chicken-run, in which a hundred and fifty fowls were kept. Early one morning one of these Cuckoos flew into the mango-tree, and as the shadow of the Cuckoo fell across the enclosure, a panic seized the fowls, which flew and ran *en masse* against the wire-netting with a bang; there they crowded and trampled upon each in the greatest confusion. They take no notice of the crows passing overhead or perched in the nearby palms. Undoubtedly the Cuckoo was mistaken for a hawk (Lumbo, 25. ix. 18).

*COCCYSTES GLANDARIUS* Linn.

The Great Spotted Cuckoo, of Europe, was first seen about September 1917, when a pair flew over the camp at Morogoro. Later, a male was shot on 27. x. 17 and another on 29. i. 18. A gaudily-coloured grasshopper (*Zonocerus elegans*) was found in fair numbers in its crop.



*COCCYSTES CAFER* Licht.

The African Pied Crested Cuckoo was collected at Morogoro (10. xii. 17) and Lumbo (22. vii. 18); at the latter place an egg was found in the nest of a Babbling Thrush (*C. kiriki*), as already mentioned (22. x. 18).

*CUCULUS CANORUS* Linn.

The European Cuckoo was twice obtained at Morogoro in February 1918 (12th and 26th). The birds were flying across the railway-line from south to north about a mile outside the town.

*LYBIUS ZOMBÆ* Shelley.

Were very common at Lumbo, going about in pairs at the time of my stay. Perched on the bare branches of the baobabs, they went through the most extraordinary courting (?) antics, accompanied by cries no less unique (Lumbo, 11. vii. 18).

*TRICHOLÆMA LACHRYMOSA* Cab.

The Black-faced Barbet was collected at Morogoro (11. vii. 17) and Dodoma (22. xii. 18). Indian corn was found in the stomach of one of the specimens from the first locality.

*TRACHYPHONUS EMINI* Reichw.

Common at Dodoma, where they were going in pairs, bowing and singing to one another. A nest with a single young one was found in a hollow thorn-tree (Dodoma, 5. xii. 18).

*CHALCOPELIA CHALCOSPILOS* Wagl.

Green-spotted Dove. Two eggs in nest (Lumbo, 24. ix. 18).

*TURTUR SENEGALENSIS* Linn.

Laughing Dove. Two eggs in nest (Morogoro, 1. viii. 17).

*TYMPANISTRIA TYMPANISTRIA* Temm.

Two eggs in nest (Kabete, 24. v. 15).

*PŒCEPHALUS FUSCICAPILLUS* Verr.

I followed a Brown-headed Parrot to a blasted tree, in which was a woodpecker's hole some 20 feet from the ground. Failing to get my hand in, I returned in the evening with two boys, who chopped the hole open after half-an-hour's labour. One of the stupid fellows placed the three large white eggs in his handkerchief, put same in his pocket and slid down the tree, breaking all three, which were perfectly fresh (Morogoro, 25. vi. 17.)

The species was also collected at Dar-es-Salaam and Lumbo; at the latter place I had a young one, which was very tame and, though loose, made no attempt to fly away.

## AGAPORNIS PERSONATUS Reichw.

Parties of this handsome little Love-bird flew about with great rapidity, screaming noisily; they were first met with at Kongwa. They were nesting in the holes of a baobab-tree, whose apertures they had apparently partly closed with a defence of thorns. Two eggs were found at the foot of the tree side by side, and measured  $\frac{5}{8} \times \frac{3}{4}$  inches. How they came to be there I cannot say, for they contained embryos nearly ready for hatching (Kongwa, 26. iv. 17).

## BUBO AFRICANUS Temm.

The Spotted Eagle-Owl was collected at Morogoro and Lumbo. At the latter place one was being mobbed by a flock of crows, which had driven it from the shelter of the bush and were pursuing it through the mangroves on the sea-shore. It alighted on a sand-bank, and was encompassed by a circle of crows, cawing with outstretched necks. The group would have made a unique photograph (Lumbo, 3. ix. 18).

## PANDION HALIAËTUS Linn.

The Osprey was found nesting at Lake Naivasha with young on 16. vii. 15.

## FALCO BIARMICUS Temm.

A female of the South African Lanner was shot whilst devouring a chicken in the topmost branches of a baobab-tree (Morogoro, 11. xii. 17). As already mentioned, the cock-bird was shot with a Kingfisher in its claws (Morogoro, 16. i. 18).

## FALCO CUVIERI Smith.

The African Hobby was shot while eating a Yellow Wagtail (*Motacilla campestris*) (Morogoro, 31. x. 17).

## DISSODECTES DICKINSONI Selater.

Dickinson's Kestrel, shot at dusk in a baobab-tree, was found to have beetles, locusts, and a praying mantis in its stomach (Morogoro, 18. vii. 17).

## CERCHNEIS TINNUNCULUS Linn.

The Common Kestrel was very common at Morogoro and Dodoma; at the latter place particularly it was rarely that there was not one in sight, usually sitting on *Euphorbia* bushes, which were scattered about the thorn-bush. One which I had in captivity thrived well on the remains of specimens which I was preserving. On one occasion, hearing a succession of screeches outside my tent, I ran out to see another Kestrel rise from the cage and fly to a tree near by. The captive bird was clinging to the wire-netting of its extensive run and screeching, being answered by the bird in

the tree for some minutes. Nearly a month later a flight of locusts visited the neighbourhood, and my bird exhibited such excitement that I released it to see what it would do. Flying straight to a large tree in the middle of the camp, it captured a locust; for the next half-hour it remained about the tree, taking short flights after the insects and returning to its perch to eat them. The following were found in the stomachs of specimens collected:—A lizard (*Eremias spekii*) and skink (*Mabuia varia*) and many locusts in one (Morogoro, 4. xii. 17); a lizard (*Latastia longicaudata*) (Morogoro, 5. ii. 18); a small bird (Dar-es-Salaam, 17. xi. 18); a rat and lizard and a parasitic worm (*A. rectovaginata*) (Dodoma, 6. xii. 18).

#### PERNIS APIVORUS Linn.

The Honey-Buzzard was twice shot at Morogoro (23. ii. & 1. iv. 18); both were females, the former with grey head, the latter with brown. In the stomach of the former were found a large number of pupæ and grubs of the grey hornet (*Belonogaster griseus*). It has been said that the feathers around the eyes of this Buzzard protect it from stings, but anyone who has seen the long stings of *Belonogaster* might be forgiven for doubting it.

#### ELANUS CÆRULEUS Desf.

The Black-shouldered Kite—a rare visitor to England—is comparatively common in the East African bush, where its dove-coloured plumage makes it look something like a sea-gull when on the wing. Specimens were obtained at Nairobi, Dodoma, Morogoro, and Lumbo. In the stomach of one was a mouse skull, beautifully cleaned and undamaged (5. ii. 18).

#### AQUILA RAPAX Temm.

The Tawny Eagle was shot at Morogoro (9. ii. 18) and Dodoma (6. xii. 18). The former had its stomach full of putrid goat's flesh, and the latter with bullock flesh and offal thrown out from the slaughter-house, where it was keeping company with vultures and kites. It had a parasitic worm (*Ascaris depressus*) in its stomach. On the road from Bissel to Longida, I rode up to an Eagle which was feeding on a dead mule. It allowed me to approach within 30 feet and, when I reined-up, looked at me for a moment, and then went on coolly tearing off strips of flesh with its beak, which it then transferred to its claws, to be held whilst rendered still smaller. In the Kedong Valley two young Eagles, just fledged, were seen sitting on the rocks at the base of the towering cliff, where their nest evidently was (17. vii. 15).

#### LOPHOAËTUS OCCIPITALIS Daud.

This Crested Eagle was found to be nesting in February. The nest was situated in a tree at a height of 80 feet from the ground. The cry of the old birds when one approached reminded me of an

English Sparrow-Hawk's note when disturbed. A few days later the birds began sitting. It was quite impossible to reach the nest, not merely because there was not a branch for 60 feet up, but because a swarm of bees nearly two feet in length were under the junction of the first branch and the trunk, whilst a second swarm hung from the big limb on which the nest was placed, about 30 feet from the main stem (Morogoro, 20. ii. 17).

MELIERAX GABAR Daud.

Gabar Goshawk. The feet of three birds were in the crop and stomach; they appeared to be those of Grass-Warblers (Morogoro, 2. vi. 17). The melanistic form was obtained a few days later at the same spot (Morogoro, 5. vi. 17).

ASTUR SPHENURUS Rüpp.

Stomach of Rüppell's Goshawk was found to contain locusts (Morogoro, 12. vii. 17).

ASTUR TACHIRO (? NYANZÆ Neum.).

Probably it was this race of the African Goshawk which I obtained at Nairobi (20. x. 15) and Morogoro (20. xi. 17). I found the nest of this species on November 17th; it was situated at the top of a tree whose bark was studded with thorns; the tree was on the banks of a stream in thick bush. On November 20th, I revisited the nest at daybreak and saw the hen feeding the young; she was very shy and, being disturbed, did not return. In the evening she was on the nest, but slipped silently away as we approached. We had brought ropes, which assisted the native in his ascent; climbing was a very tedious business, as the thorns had to be cut away all up the trunk. The two young in the nest were of very different size, and one would think there was quite a week's difference in their ages; the smaller bird was still in the down stage.

After removing the young, I sat down in the gathering gloom and watched the dark outline of the nest silhouetted against the sky; an indistinct "something" sailed past, and the next moment the mother could just be seen alighting on the edge of the nest. She had scarcely time to close her wings when I fired, and she fell forward dead into the empty nest. This involved another climb for the boy. After gathering up the rope, hatchet, and spoils we stumbled back through the bush to camp, guided by the gleaming thread of water which lay in the river bottom.

I skinned the bird at once—it was in fine condition—and then fed the young with the flesh cut into strips; they ate with avidity. Next morning I fixed up a very fair imitation of their home on the top of a bush in the python's cage. On the 28th they began to feed themselves, and were fond of standing up in the nest.



They held down scraps of meat in their claws, tearing it into still smaller scraps with their beaks. Up to this time they were fed on the flesh of monkey, lemur, rat, bullock, kite, hawk, egret, hornbill, kingfisher, roller, wheatear, wagtails, weaver, crow, puff adder, and chameleon. All these seemed to agree with them except that of the bullock and the chameleon fat, both of which they disgorged.

On December 1st the larger of the young Goshawks was just beginning to fly about the cage when it disappeared; the 12-foot python must have eaten it. I had kept him so gorged with dead fowls that I never imagined he would molest them. The following day, hearing my monkeys making a great outcry, I hastened out to find the python sliding silently towards the bush on which the nest had been placed. I removed the remaining hawk just in time, for on passing back to my tent I saw the python had raised itself to the nest over which he was running his snout. Having nowhere else to keep it, I left the bird in an open grass hut.

On December 7th it took trial flights about this hut. When the two young ones had been in the python's cage I had been much puzzled by finding their excreta about 4 feet from the nest. Now, I observed the remaining bird hop out of the box in which it was, turn round on the edge, cock up its tail and discharge the fluid "whitewash" to a distance of 3 feet. This shows how they are able to keep the nest clean. It disgorges pellets of fur  $1\frac{1}{2}'' \times \frac{5}{8}''$  in size.

The young bird was not in the least like its parent, having large pear-shaped brown blotches on the breast like *F. biarmicus*. The mother, of course, has transverse fine striations. On December 13th I missed the bird; the night before it had flown about 500 yards and stayed out all night. Someone accidentally discovered it in a rubber-tree, and, in trying to recover it, struck it with a butterfly net, which caused its death the following night, as a small clot of blood was found on the spine when dissected.

#### BUTASTUR RUFIPENNIS Sundev.

A Buzzard Eagle was fairly plentiful at Morogoro and Dodoma. The stomach of a specimen examined contained scarabs (Morogoro, 31. i. 18).

#### CIRCAËTUS PECTORALIS Smith.

In the stomach of a Black-breasted Harrier Eagle was a pellet of rodent fur, in its gullet was a Hissing Sand Snake (*Psammodphis sibilans*) 2 feet in length, its tail being doubled back for about 9 inches; it had been swallowed head first. Curiously enough, four days earlier I stalked a handsome Barred-breasted Eagle in the same tree in which I shot this specimen. On raising my head when within range I lost sight of it, but a



minute later it rose from the mealies two hundred yards from the tree, with a snake in its talons. It came so low over my head that I was able to recognise the snake as a Hissing Sand Snake. The Eagle then ascended in great spirals, taking the snake from its talons with its beak and gulping it down as it ascended. I was so interested that I forgot to shoot till the bird had finished, and then when I did fire, missed, so that I was unable to identify the Eagle, which was an unfamiliar one (Morogoro, 4 & 8. vi. 17).

#### ASTURINULA MONOGRAMMICA Temm.

Variously known as the African Buzzard-Eagle, Lesser Whistling Hawk, and One-streaked Hawk. The first name from a popular point of view is a very absurd appellation conveying the idea of great size. One-streaked Hawk seems to me the best popular name conveying some idea of the bird. A female shot at Morogoro had a Side-walking Spider (*Palystes* sp.) in her stomach. A male was obtained a few months later (Morogoro, 2. iv. & 9. vii. 17).

#### CIRCUS MACRURUS Gmel.

In the stomach of a Pale Harrier was found a young snake (*Rhamphiophis oxyrhynchus*) and a skink (*Mabuia striata*), whilst in that of a second were three species of lizards (*Eremias spekii*, *Gerrhosaurus flavigularis*, and *Mabuia striata*). Here the Pale Harrier seems to prefer a reptilian diet (Morogoro, 31. i. & 28. ii. 18).

#### MELANOPHOYX ARDESIACA Wagl.

The Black Heron feeds along the shore at Dar-es-Salaam when the tide is out; it was there very difficult of approach. On one occasion, as I was returning home, one of these small Herons flew over the causeway and dropped on a muddy flat not far from where there was some grass. I was on the far side of the water and immediately made for the place. The bird I found was performing some very curious antics. Running swiftly forward for about six steps, it abruptly halted, placed its beak to the ground, and raising its wings, brought them forward and downwards, so that for a moment its head was entirely hidden by the outspread wings which were brought down to the mud. This it repeated again and again until, reaching the water, it turned about and practised its steps in the opposite direction.

I imagined that it was a cock performing some courting display, but on skinning found it to be a hen. Taking advantage of each moment when its head was concealed, I wriggled forwards through the grass till within range, when I dropped it, very dead indeed, but a perfect specimen (Dar-es-Salaam, 1. vii. 18). Six months later I saw these birds performing the same antics on the fore-shore opposite the ruined Governor's Palace.

*ARDEA MELANOCEPHALA* Vig. & Child.

The Black-headed Heron was met with at Dar-es-Salaam (26. vi. 18), Morogoro (29. xi. 18), and Tabora (13. xii. 18). At Tabora they were nesting in a great tree in the midst of cultivated ground, the birds winging their way home of an evening from their feeding grounds. One of the Morogoro specimens was shot stalking about a stubble field, and its stomach on examination was found to contain the remains of rats, apparently five in number.

*ARDEA CINEREA* Linn.

The Common Heron of Europe was twice collected at Dar-es-Salaam (5. vii. & 19. xi. 18), the circumstances being as follows:—

Just 60 feet below the bank on which our house is built, and perhaps a hundred yards away, lies a one-time estuary of the sea; the fresh water is now shut off from the sea by a causeway, but a series of large pipes still allow of communication between the two at high tides, after which infusion the water is brackish. Here various waterfowl are wont to feed on the freshwater shrimps and small fish, including the Mud Skipper (*Periophthalmus* sp.), which is present in large numbers; while at daybreak each morning a pair of herons are to be seen standing in the shallows.

Every morning for eight days past I tried to stalk them, but they were too wary, taking to wing whilst one was still a hundred yards off. Once disturbed the birds would circle round in the blue above, and then, heading over the causeway, would fly seawards, doubtless to recommence feeding in one of the quiet bays or lagoons with which the coast abounds. However early I arrived, the birds were there before me, but determined to succeed this morning I started out at 4 o'clock.

When I left the house it was pitch dark except for a waning moon whose faint beams were reflected on the shimmering surface of the dark water. Stumbling around the estuary in the spongy soil where crickets were shrilling away, I reached the far end, and was carefully withdrawing my feet from a particularly boggy piece of ground, when suddenly I became aware of the presence of a bird standing motionless in the shallow water scarcely 30 feet away.

I hesitated for a moment, lest in the deceptive light the bird might be nearer or farther than it appeared, as I was anxious not to damage the skin; also the report of the gun echoing across the water might disturb the slumbers of our neighbours occupying the houses along the opposite bank. Ere I had made up my mind the heron rose with a hoarse squawk, and, spreading its great wings, disappeared into the darkness. A smaller species arose and settled again further out.

Pursuing my way round the estuary I arrived at an old stranded buoy close to which there was a favourite fishing-ground

of the birds. Sure enough, before I was within fifty yards of it, the bird again arose and departed across the water. Its mate generally fished near a stone some little way further along the bank, and there I espied it; the recognition was mutual, and it winged off to a promontory where I could just distinguish it standing in the water.

In pursuance of my original intention, I now lay down in the wet grass within range of the stone and here waited for half-an-hour until day broke behind a row of tall palms, which later formed a lovely picture silhouetted against the rosy dawn. The grass, however, was very short owing to the activities of the Sanitary Corps, so that as the light increased, realising how conspicuous I must soon appear, I crawled away to a shallow irrigation ditch fringed with longer grass and within range of the buoy. Half-an-hour passed which the mosquitoes relieved of all monotony. It was quite a new point of view to see them arrive, like so many vultures outlined against the sky, and then to alight on the stems of grass which were already burdened with dew.

At 6 A.M., reveille sounded and some K.A.R. askaris from a neighbouring camp came down to wash clothes, but instead of taking to flight at their approach, my heron, now clearly to be seen across the shining water, sedately stalked further out. My patience well nigh exhausted, I rose on one elbow, and, seeing how light it had become, was on the point of giving up when another native came down to the opposite bank, and as it appeared probable that he would pass near the bird I resolved to wait a little longer and crouched low again.

A hoarse cry from the Heron caused me to look up; afar I beheld the big bird rising from the water. Down I ducked, face and hand well into the grass, not daring to move lest I should attract attention. A few moments of anxious suspense, then swish, swish, swish sounded its pinions close overhead, as it circled round preparatory to alighting. Then came a gentle splash as it struck the water.

Very cautiously I raised my head and looked through the grass stems, where, not 40 feet away, stood my victim, suspiciously turning its head from right to left as it strode along. Being cramped and stiff, I feared to raise my gun lest I should muddle things, and the weary hours of waiting be wasted; so again I lay quiet until, in its walk, the bird should come into line with the barrels of the gun as it lay on the ground—bang!

Overhead a raucous squawk and the sound of wings! What then. Surely I could not have missed. Hastily and awkwardly I rose to my feet. No! There lay the victim of my murderous early rising floating quietly on the water, stone dead; a shot had passed through its neck and a single spot of blood showed on one leg. It floated listlessly to and fro as I waded out to bring it in. Far out towards the sea a speck in the sky was all that was to be seen of the other bird, which, all unknown to me, had come up

close behind where I was lying, and, at the sound of the shot, had risen with a cry. The dead bird measured 59 inches from tip of beak to the tip of its longest claw (Dar-es-Salaam, 5. vii. 18).

*SCOPUS UMBRETTA BANNERMANNI* C. Grant.

East African Hammer-head. At Dar-es-Salaam I found a nest from which the young had just flown, according to the natives living about 30 feet away. They said that the bird had bred there for many years; its nest, in the fork of a tree, was scarcely 10 feet from the ground and easily accessible. I was surprised that the thrifty natives had not pulled down the load of sticks for firewood (8. ii. 19).

*CICONIA CICONIA* Linn.

The White Stork was only met with once and then in thousands. It was at Morogoro (19. ii. 18), when about 4 P.M. my attention was drawn to a great flock of birds high in the air; others were coming round the western spur of the Uluguru Mtns. from a S.W. direction. It was a most wonderful sight, and reminded one of the Gannets flying about the Bass Rock, with this difference: that in lieu of the limitless sea for a background, one had the forest-clad slopes of the Uluguru reaching up into the clouds. And over the top and down the slopes, or circling mid the clouds, still the birds came, the specks grew larger and larger, then showed white and black until finally they were recognisable as storks.

Thousands upon thousands came sailing through the air without visible effort. By scores they settled in the trees, stiff and erect, their white plumage against the forest foliage forming a not easily forgotten picture. It was very evident what had brought them, for they pursued the locusts (which had appeared the day before) on the wing, swallowing them in wholesale fashion. In flight they carried their red legs straight out behind, but when intending to alight, they were allowed to hang down and swing freely to and fro like a parachute coming to earth. There is a curious mechanism of the knee-joints, necessitating the leg being out straight or bent at right angles; in either position it locks. After death, if the leg was placed in any other position, it flew to one or the other of these of its own accord.

Millions upon millions of the locusts continued steadily driving past like rain; the air was vibrant with the noise of their flight and with the steady pinion-beats of the pursuing storks. Others of the insects settled on the vegetation, which was a-rustle with them as they hopped, or took short flights, out of one's way. The measurement of the outstretched wings of one of the storks was 6 feet 3 inches.

*ABDIMIA ABDIMII* Licht.

The following morning the storks were still about, and circled over the hospital, where they were made targets of by a number



of foolish officers, who blazed away at them with service rifles. One of those shot was brought to me, and I recognised it as the White-bellied Stork (*A. abdimii*). When one considers what myriads of locusts such thousands of birds must consume—the stomachs of those shot being distended with the insects,—what folly it is to destroy them needlessly.

Someone reported having seen a Secretary Vulture among the storks, which were picking up locusts among the stubble of a mealie-field. Numbers of hawks, eagles, and rollers were harrying the locusts also.

*CREX CREX* Linn.

The Corn-Crake or Land-Rail was taken at Nairobi during the first nine days of May 1916 and 15. iv. 19.

*COTURNIX DELEGORGUEI* Hartl.

A Harlequin-Quail was obtained under rather peculiar circumstances, and shows how close these birds will squat. I was walking across a patch of grass-grown land in Nairobi when something rustled at my very feet; jumping to one side, expecting to see a snake, I found it to be a quail that I had trodden upon inadvertently (Nairobi, 2. vii. 15).

The following records of European migrants may be of interest:—

*CHARADRIUS ALEXANDRINUS* Linn. Kentish Plover. Dar-es-Salaam (13. i. 19).

*CHARADRIUS HIATICULA* Linn. Ringed Plover. Nairobi (12. x. 15); Dar-es-Salaam (14. i. 19).

*TRINGA SUBARQUATA* Güld. Curlew-Sandpiper. Dar-es-Salaam (14. i. 19).

*TRINGA MINUTA* Leisl. Little Stint. Lumbo (5. x. 18).

*CALIDRIS ARENARIA* Linn. Sanderling. Dar-es-Salaam (15. i. 19).

*TOTANUS HYPOLEUCUS* Linn. Common Sandpiper. Lumbo (27. vii. & 4. ix. 18).

*NUMENIUS PHÆOPUS* Linn. Whimbrel. Dar-es-Salaam; often seen in January 1919, but not collected.

*NUMENIUS ARQUATUS* Linn. Curlew. Dar-es-Salaam (7. vi. 18); Lumbo (25. vii. 18).

*HIMANTOPUS HIMANTOPUS* Linn. Black-winged Stilt. Tabora; seen only (11. xii. 18).

*HÆMATOPUS OSTRALEGUS* Linn. Oyster-catcher. Dar-es-Salaam; often seen during 1918.



38. On the Myology and Classification of the Wombat, Koala, and Phalangers. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society.

[Received August 1, 1922: Read November 7, 1922.]

(Text-figures 31-43.)

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*Introduction.*

The most remarkable features in the existing classifications of the Diprotodont Marsupials\* are the positions assigned to the Wombat, Koala, and Phalangers. Some zoologists have included the Koala in the Phalangeridæ and kept the Wombat separate. Others have included the Koala and Wombat in the Phascolarctidæ. And others again have formed three families—Phalangeridæ, Phascolarctidæ, and Phascolomyidæ. It is evident, therefore, that there is considerable difference of opinion as to the true positions of these animals. To form a lasting and natural classification one must examine all anatomical data, so as to exclude convergent and adaptive characters, and those which represent varying degrees of persistence of primitive conditions which were present in their common ancestor. The exclusion of these conditions, leaves us with data which are of value for purposes of classification. And these can be divided into major and minor groups. Minor characters are employed to emphasise the classification based on major ones.

In the examination of animals received at the Society's Prosectorium† I observed so many points in their myology hitherto unrecorded, or different from existing accounts, that I have considered it fit to set them down as a separate section in this paper. As the anatomy of the skeleton, teeth and viscera is already well known I have simply mentioned the most distinctive characters in the section on classification.

MYOLOGY.

*Muscles of the Head and Neck.*

The *Platysma* in all species is muscular in the face and neck. It is continuous with the facial, orbital, and auricular muscles,

\* Pocock (9) and Osgood (7) have reproduced most of the systems of classification which have been proposed.

† *Phascolomys mitchelli* (♂ ♀), *Phascolarctos cinereus* (♀), *Phalanger orientalis* (adult female and female mammary fetus), *Pseudochirus peregrinus* (♀ ♀ ♀). Many points in the anatomy of *Trichosurus vulpecula* have been described by me in a former paper (10).

but the fusion is best marked in *Phascolarctos*. Fibres run to the pads of vibrissæ, but none are continuous with the well-developed muscles in the labial labrets in *Phascolomys*. There is no essential point of difference between the platysma in these forms and the *Phalangeridæ*.

*Masseter*:—The general form is similar in *Phascolomys* (text-fig. 31 A) and *Phascolarctos*\*; in the former the anterior border is thick and muscular, but it is thin and tendinous in the latter. In *Phalanger* (text-fig. 31 B) and *Pseudochirus* (text-fig. 31 C) the form differs from the above: in the former the surface is subdivided by sulci into three parts, but it is undivided in the latter.

*Pterygoids*:—Macalister (5) observed that the external pterygoid is small and fused with the internal pterygoid in *Phascolarctos*, but I found it separated and well developed in all forms.

*Digastric* (text-figs. 32–34 †):—In *Phascolarctos* it is monogastric and fused with the mylo-hyoid, genio-hyoid, and omo-hyoid; and it is inserted into the mandible. I have already shown that it enters into a sheet with mylo-hyoid and sterno-hyoid (10), and I believe that the lateral fibres of the sheet correspond to the digastric. Young (14) described two bellies and a tendinous inscription. In *Phascolomys* the broad anterior bellies conceal the mylo-hyoid, and strong intermediate tendons unite them to the posterior bellies. In *Phalanger* the broad anterior bellies do not completely cover the mylo-hyoid, and the posterior bellies are fusiform. In *Pseudochirus* the monogastric muscles conceal the greater part of the mylo-hyoid. In no species has the digastric any connection to the hyoid bone. There is, therefore, a close resemblance between the digastric muscles in *Phascolarctos* and *Pseudochirus*.

*Mylo-hyoid* (text-figs. 32–34, M-H.M):—In *Phascolomys* and the *Phalangers* the mylo-hyoid runs from the mandible to the hyoid bone. But in *Phascolarctos* it does not get any attachment to the hyoid. In my specimen it is fused with the sterno-hyoid; and there is, in reality, a sterno-mandibularis. Young (14) does not mention fusion of mylo-hyoid and sterno-hyoid, but notes that the mylo-hyoid has no attachment to the hyoid bone.

*Omo-hyoid* (text-figs. 32–34, O-H.M):—In *Phascolomys* and the *Phalangers* it is attached to the hyoid bone, but no central tendon is present. In *Phascolarctos*, however, it avoids the hyoid bone and passes forwards to enter the tongue, wherein it forms a lingualis.

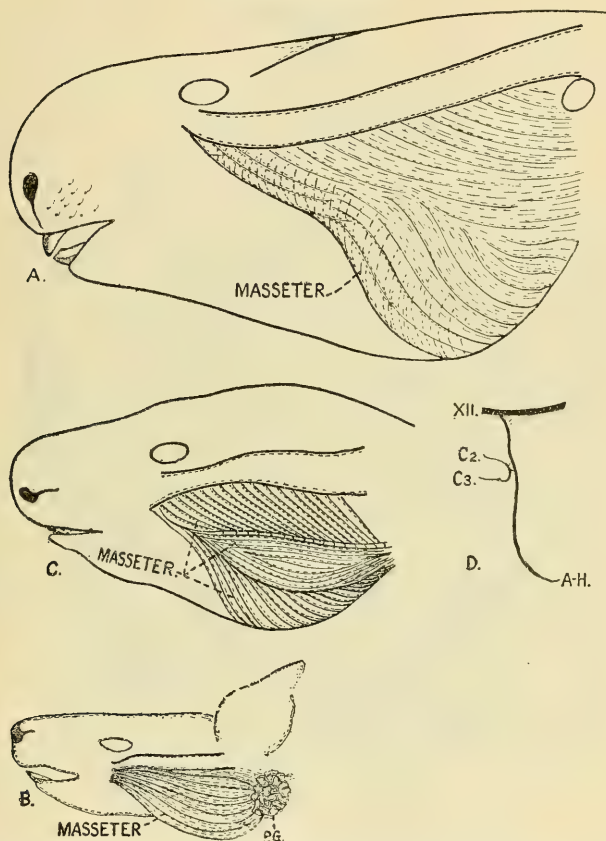
The ansa hypoglossi, which supplies the omo-hyoid and pre-tracheal muscles, is derived from the cervical plexus alone in *Phascolarctos*, *Phascolomys*, and *Pseudochirus*. In *Phalanger* I observed the nerve receiving connections from the first three cervical and the hypoglossal nerves (text-fig. 31 D).

\* P. Z. S. 1921, p. 548, text-fig. 53.

† *Ibid.*, p. 549, text-fig. 54.

*Pretracheal Muscles*.—In all the animals described in this paper the sterno-hyoid muscles could easily be separated from the subjacent sterno-thyroids. The sterno-hyoids are fused in *Phascolarctos* and have no connection to the hyoid bone, so they

Text-figure 31.



The masseter muscle in *Phascolomys mitchelli* (A.), *Pseudochirus peregrinus* (B.), and *Phalanger orientalis* (C.); D: the ansa hypoglossi in *Phalanger orientalis*.

C2 and C3: cervical nerves; A-H: ansa hypoglossi; P.G.: parotid glands  
XII: hypoglossal nerve.

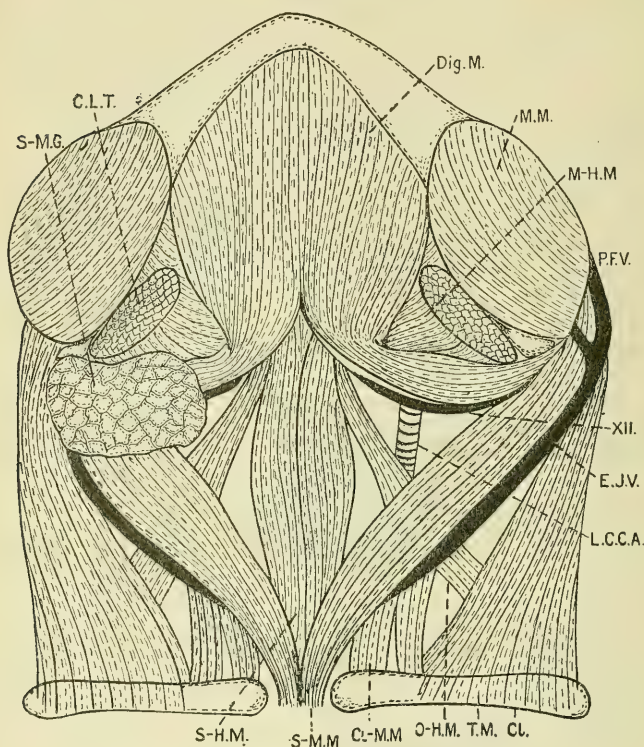
play no part in its movements. But in all other species they are separate and receive an insertion to the hyoid. The sterno-thyroids are essentially similar in all.

*Hyoglossus*.—Young (14) describes it as a transverse band, bridging over the genio-glossi, and having no hyoid attachment

in *Phascolarctos*. I did not, however, observe this band at all. Macalister (5) regarded it as a piece of the mylo-hyoid. In *Phascolomys* and the Phalangers it runs from the hyoid bone to the tongue.

It is, therefore, evident that the Koala has many traces of

Text-figure 32.



Anatomy of the neck in *Phascolomys mitchelli*.

CL: clavicle; CL-M.M: cleido-mastoid; C.L.T: cervical thymus; Dig.M: digastric; E.J.V: external jugular vein; L.C.C.A: left common carotid artery; M-H.M: mylo-hyoid; M.M: masseter; O-H.M: omo-hyoid; P.F.V: posterior facial vein; S-H.M: sterno-hyoid; S-M.G: submaxillary gland; S-M.M: sterno-mastoid; T.M: trapezius; XII: hypoglossal nerve.

primitive lamination in its platysma, mylo-hyoid, sterno-hyoid, and hyoglossus muscles. And in these conditions it differs entirely from *Phascolomys* and the Phalangers.

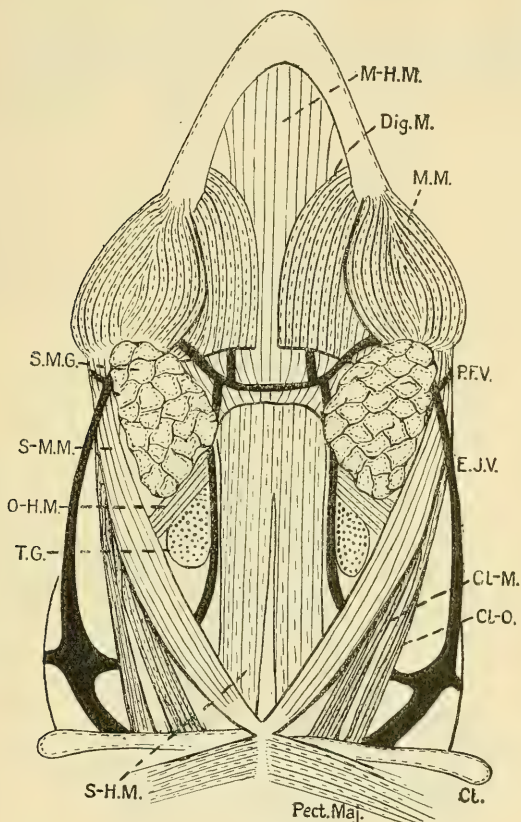
*Sterno-mastoid, Cleido-mastoid, Cleido-occipital* (text-fig. 32, S-M. M, Cl-M, Cl-O):—All are present in the Phalangers, but the



last is absent in *Phascolarctos* and *Phascolomys*. The insertion of sterno-mastoid and cleido-mastoid is into the occipital crest.

*Genio-hyoid*:—In my specimen of *Phascolarctos* it runs from the symphysis of the mandible to the hyoid bone and thyroid cartilage, so it is in reality a genio-hyo-thyroid. This arrangement

Text-figure 33.



Anatomy of the neck in *Phalanger orientalis* (adult).

CL-O: cleido-occipital; Pect.Maj: pectoralis major; T.G: thyroid gland. Other letters as in last figure. In a mammary foetus the cervical thymus concealed the lower part of the neck. Note the vertical anterior jugular veins and the horizontal vena transversa.

differs from Young's account (14). As no other thyro-hyoid muscles are present, they are probably replaced by a part of the genio-hyoid.

The genio-hyoids and stylo-hyoids are the only muscles



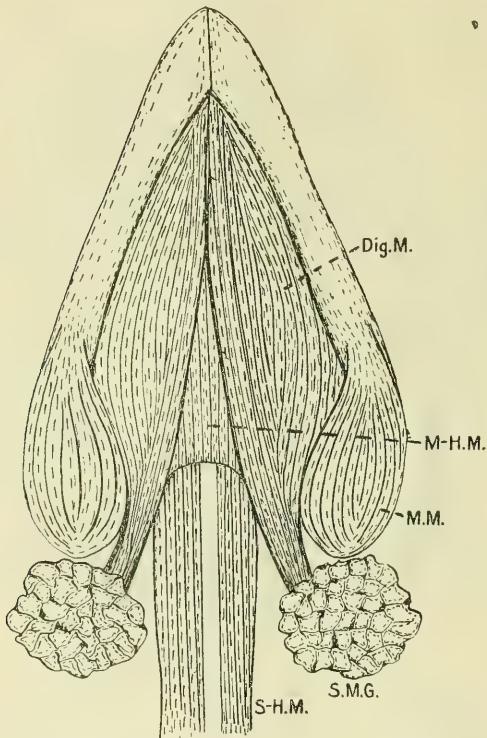
attached to the hyoid bone in my specimen of *Phascolarctos*, for the pharyngeal constrictors have no hyoid origin.

*Scaleni*:—In all forms the scalenus anticus is absent, as the scalene group is behind the brachial plexus. The scalenus medius and posticus are present.

*Splenius*:—In *Phascolarctos* it is divisible into two parts (capitis and colli), but it is a single sheet in *Phascolomys* and the Phalangiers.

*Prevertebral Muscles*:—Young (14) described these muscles in *Phascolarctos*, and pointed out that they are more or less

Text-figure 34.



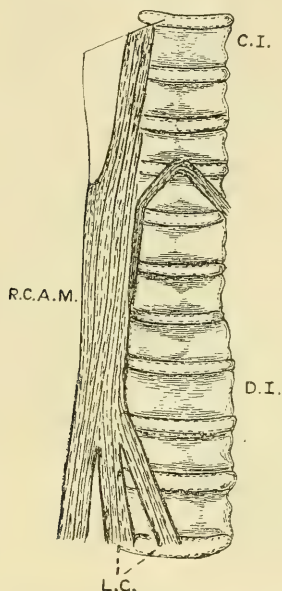
Anatomy of the neck in *Pseudochirus peregrinus*.

Letters as in text-fig. 32.

inseparable. The rectus capitis anticus major is the largest; it runs from the bodies of the first three dorsal vertebræ and all cervical transverse processes to the basi-occiput. Rectus capitis anticus minor cannot be isolated. Longus colli consists of fibres running between the bodies and transverse processes of the first

three dorsal and cervical vertebræ. In *Phascolomys* I observed similar fusion of these muscles. A single thick muscular sheet extends from the third dorsal vertebra to the basi-occiput (text-fig. 35). A small bundle of fibres becomes detached, and runs to the front of the third cervical vertebra when it fuses with the bundle from the opposite muscle. The main mass, in my opinion, represents rectus capitis anticus major. The mesial part represents longus colli, and the rectus capitis anticus minor is absent. In *Phalanger* there is more separation between the longus colli and rectus capitis anticus major, and there is no rectus capitis anticus minor. But in *Pseudochirus* there is considerable

Text-figure 35.

Prevertebral muscles in *Phascolomys mitchelli*.

Letters in text.

fusion. It appears, therefore, that the conditions in *Phalanger* do not adhere so much to the primitive condition as do those in *Phascolarctos*, *Phascolomys*, and *Pseudochirus*.

#### *Muscles of the Back, Thorax, and Abdomen.*

*Trapezius*:—In all forms the origin extends from the occiput to the seventh dorsal spine, although Young (14) gave the eighth spine as well in *Phascolarctos*. The clavicular insertion varies, however. In *Phascolarctos* and *Pseudochirus* most of the fibres go to the clavicle, but some cross it and run to the clavicular deltoid,

In *Phascolomys*, on the other hand, most of the fibres cross the clavicle and fuse with the clavicular deltoid; and some fuse with the cleido-mastoid. In *Phalanger* the conditions are intermediate. The scapular insertion is, however, similar in all. And in no case is there a tendinous intersection where the fibres cross the clavicle. The fusion of the trapezius and clavicular deltoid is a persistence of the primitive lamination, and is best marked in *Phascolomys*.

*Rhomboideus*:—In all forms it is an indivisible sheet whose origin extends from the occiput anteriorly to the thoracic region posteriorly, and it thickens from before backwards. It reaches the fifth dorsal spine in *Phascolomys*, but stops at the third in *Phascolarctos*, *Phalanger*, and *Pseudochirus*. As the rhomboideus shows no division in any of these animals they all exhibit a persistence of the primitive condition of the muscle.

*Latissimus Dorsi*:—This muscle arises from a variable number of posterior thoracic spines and the lumbar fascia, but there are neither iliac nor scapular origins. Costal slips may exist. The following origins were present in my specimens:—

*Phascolarctos*: spines 4–10; no costal origin.

*Phalanger*: spines 4–12; slip from last rib.

*Pseudochirus*: spines 4–12; no costal origin.

*Phascolomys*: spines 5–15; slips from lower six ribs.

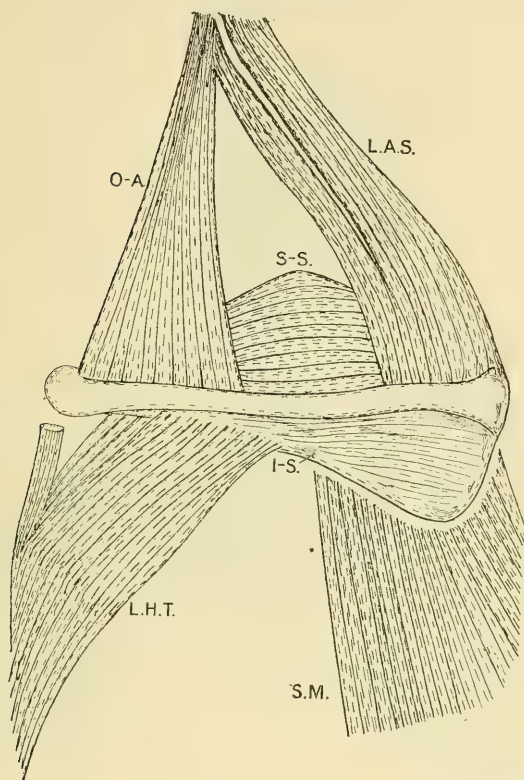
The insertion of the latissimus is very similar in all, and it is intimately connected to the teres major and dorso-epitrochlearis.

*Levator Anguli Scapulæ*:—Young (14) states that it arises from the front of the lateral mass of the atlas along with the first slip of the serratus magnus in *Phascolarctos*; but he does not mention whether it is fused with the omo-atlantic. It is inserted into the scapular spine. In *Phascolomys* I observed it arising in company with the omo-atlantic from the caudal border of the lateral mass (text-fig. 36 A). And it is closely connected to the upper part of the serratus magnus. It is attached to the root of the spine of the scapula. In *Phalanger* (text-fig. 37) it arises in common with the omo-atlantic, but is separate from the serratus magnus. It is inserted into the dorsal surface of the scapula in the anterior part of the supraspinous fossa. In *Pseudochirus*, on the other hand, it is inseparable from the serratus magnus, and its insertion never reaches the spine of the scapula. It is, therefore, evident that *Phascolomys* and *Phascolarctos* differ from the *Phalangers* in the insertion of the levator scapulæ. So the conditions of the levator scapulæ and serratus magnus are degrees of persistence of primitive lamination.

*Omo-atlantic* (text-figs. 36 & 37):—In *Phascolomys* and *Phascolarctos* it runs, widening as it goes, from the lateral mass of the atlas to the outer part of the spine of the scapula. And the lateral fibres cover the dorsal part of the shoulder joint. In *Phalanger* and *Pseudochirus* it divides into two parts—a broad mesial and a narrow lateral slip—and these are attached to the

outer half of the scapular spine. Cunningham (2) describes it as two muscles fixed to the whole length of the scapular spine in *Cuscus*. The conditions in the Phalangers cannot be due to their leading an active arboreal life, as other active animals have a single muscle. They are probably remnants of primitive laminations.

Text-figure 36.

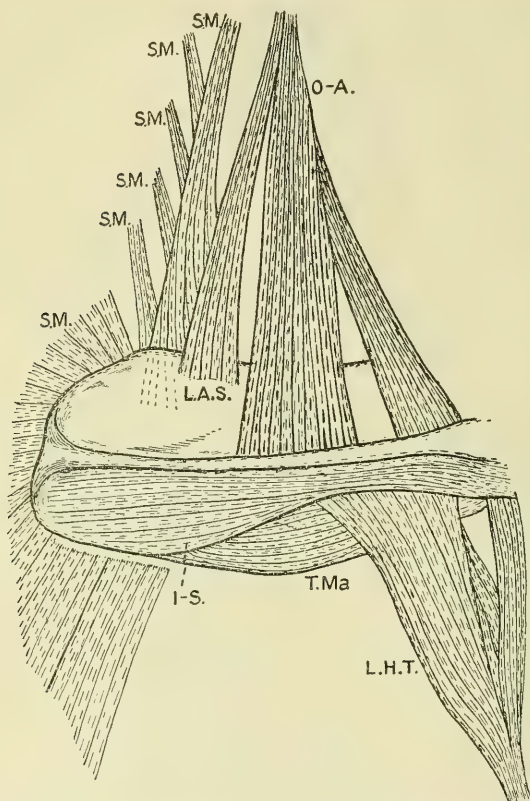
Scapular muscles in *Phascolomys mitchelli*.

I-S: infra-spinatus; L.A.S: levator anguli scapulæ; L.H.T: long head of triceps;  
O-A: omo-atlantic; S.M: serratus magnus; S-S: supra-spinatus.

*Serratus Magnus* (text-figs. 36-38):—In the Marsupialia there is a more or less intimate connection between the levator scapulæ and the serratus magnus, thus showing that these muscles are part of the same sheet. And the origin of the serratus extends from the anterior cervical to the posterior thoracic region. In *Phalanger* the origin extends from the second cervical vertebra to the seventh rib. The cervical slips are all distinct. In *Pseudochirus* there are eight thoracic slips. The cervical slips are

also coarser than the thoracic ones, but they are closer together. In *Phascolarctos* Young (14) described six cervical and nine thoracic slips, and I observed the same. But Macalister (5) recorded seven costal slips. As regards *Phascolomys*, Macalister pointed out that the cervical and thoracic parts are separate, and he described them in detail.

Text-figure 37.

Scapular muscles in *Phalanger orientalis*.

T.Ma : teres major. Other letters as in text-fig. 36.

*Intercostal Muscles*:—The number of sets of intercostals varies, as the result of variations in the number of ribs, but the characters of the muscles are essentially similar in all:—

*Phascolarctos*: ten pairs of interspaces.

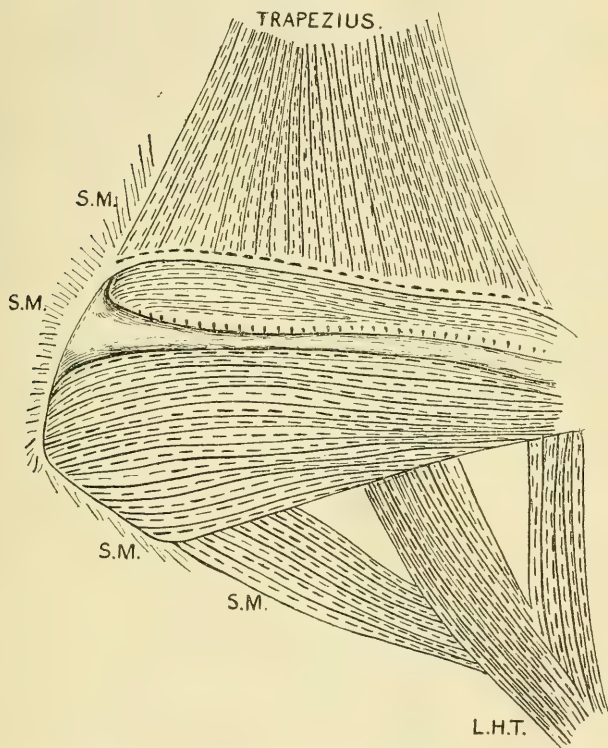
*Phascolomys*: fourteen pairs of interspaces.

*Phalangeridæ*: twelve pairs of interspaces.



*Muscles of the Ventral Abdominal Wall*:—In the Phalangers at my disposal the muscles of the ventral abdominal wall were all firmly united together and the linea alba was very obvious. The rectus abdominis had eight intersections, and the first one was so wide that there is apparently a rectus abdominis and rectus thoracis. This condition was also present in Young's specimen of *Phascolarctos* (14). In *Phascolarctos* and *Phalanger* the pyramidalis conceals the rectus, and gets one insertion into the sternum

Text-figure 38.

Scapular muscles in *Phascolarctos cinereus*.

Letters as in text-fig. 36.

and last costal cartilage, but it is not so extensive in *Phascolomys*. These animals are, however, essentially similar as regards all the muscles of the ventral abdominal wall.

*Dorsal Abdominal Muscles*:—The quadratus lumborum is well developed in *Phascolomys* and the Phalangers. In *Phascolarctos* it is more primitive, for it is practically absent, or, as Young (14) suggests, it may be replaced by intertransverse muscles connecting

the lumbar vertebræ. The *psoas parvus* exceeds the *magnus* in all forms, but the disproportion is not so great, and the *parvus* is more tendinous in *Phascolomys*. Macalister (18) describes it as a weak muscle in the latter. It is inserted into the pubis behind the corresponding marsupial bone in all forms.

*Muscles of the Anterior Extremity.*

The *Dorso-epitrochlearis* arises from the posterior border of the *latissimus dorsi* and its tendon in *Phalanger* and *Pseudochirus*, and it remains muscular to its insertion into the tip and inner border of the olecranon. In *Phascolarctos* it is thin, and a considerable part is fascial. In *Phascolomys* it arises chiefly from the tendon of the *latissimus*, and it is firmly bound down by deep fascia. When the fore-limb is abducted the muscle becomes tight soonest in the latter. And the distant extremity is more evidently continuous with the *anconeus internus* in *Phascolarctos*.

*Pectoral Muscles*:—Cunningham (2) analysed the pectoral mass, and described a *pectoralis major* composed of superficial and deep parts, a *pectoralis minor*, and a *pectoralis quartus*. In my specimens the conditions present differed in some respects from those described by Young, Cunningham, Macalister, and others.

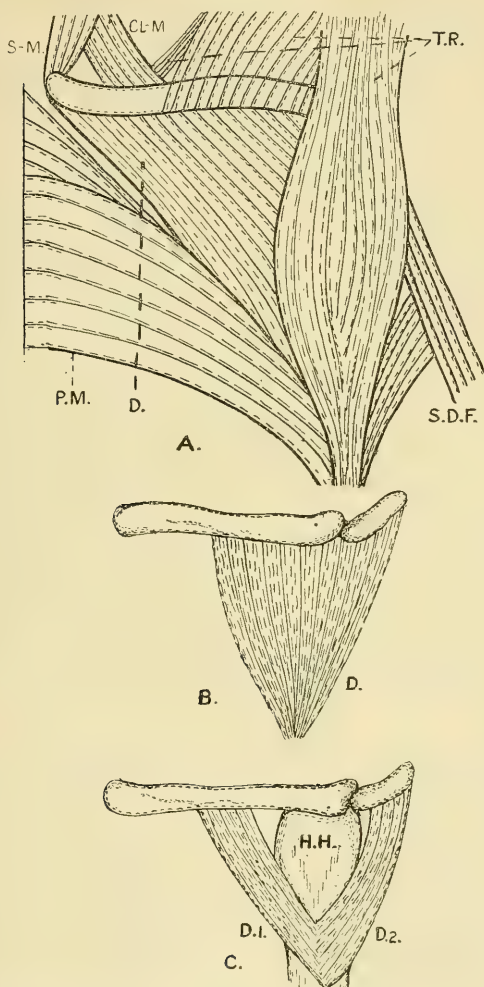
*Pectoralis Major*:—In *Phascolomys* Macalister (18) showed that the superficial part has clavicular, sternal, and costal origins. In my specimen (text-fig. 39 A) it arises from the mid-sternal line and fascia over the abdominal muscles in the infra-sternal fossa; there is no clavicular nor costal origin. It is inserted into the pectoral crest of the humerus and fuses extensively with the clavicular deltoid. The deep part arises from the manubrium sterni, crosses the *pectoralis minor* and *quartus*, and is inserted by a narrow tendon into the outer tuberosity and upper part of the pectoral crest. It is separated from the first part. In *Phalanger* the superficial part does not arise from the entire length of the sternum, but in other respects it resembles the superficial part in *Phascolomys*. The deep part has a more extensive origin from the body of the sternum. In *Pseudochirus* the conditions are similar to those in *Phalanger*, but it is difficult to distinguish the superficial part from the clavicular deltoid in the fused muscular mass. In *Phascolarctos* the superficial part has an origin from the inner third of the clavicle, so the clavicular deltoid does not reach the sterno-clavicular joint as it does in *Phascolomys*. I have already described and figured muscles resembling those in the latter in *Mandrillus leucophaeus*.

*Pectoralis Minor*:—In *Phascolomys* it arises from the posterior three-fourths of the sternum, and it is inserted into the great tuberosity, coraco-humeral ligament, and coracoid process. It remains separate from the *quartus*, but their insertions are contiguous. In *Pseudochirus* the *minor* and *quartus* are in contact throughout the greater part of their course. But in *Phalanger* and *Phascolarctos* they are separate.

*Subclavius*:—The insertion varies. In *Phalanger* it is attached

to the outer two-thirds of the anterior border of the clavicle. In *Pseudochirus* the conditions are similar to the above. In

Text-figure 39.



Clavicular muscles in *Phascolomys mitchelli* (A.), *Phascolarctos cinereus* (B.), and *Phalanger orientalis* (C.).

CL.M: cleido-mastoid; D.D<sub>1</sub>.D<sub>2</sub>: deltoid; H.H: head of humerus; P.M: pectoralis major; S-M: sterno-mastoid; S.D.F: slip of deltoid to forearm; T.R: trapezius.

*Phascolarctos* it runs to the outer sixth of the clavicle. The attachment is more extensive in *Phascolomys*, for it is fixed to the

outer sixth of the clavicle, the upper border of the acromion, and the spine of the scapula. I believe the extent of this muscle is partly due to varying degrees of functional activity.

*Deltoid* (text-fig. 39 A-C):—In *Phascolomys* the origin forms a continuous line along the whole length of the clavicle, the acromion and lateral third of the spine of the scapula. The clavicular fibres receive the trapezius, and the acromial fibres and trapezius form a powerful cephalo-humeralis. The clavicular deltoid also fuses with the superficial part of the pectoralis major, and the two are inserted into the pectoral crest. From the scapular fibres a long, narrow, strap-like band runs to the deep fascia over the radial border and dorsum of the forearm and carpus. In *Phascolarctos* the muscle is also entire, the clavicular origin is not so extensive, and the narrow band given off fuses with the supinator longus. In *Phalanger* and *Pseudochirus* the clavicular origin is not as extensive as in *Phascolomys*, the clavicular and acromial parts are separate, and no slip is given off to the forearm.

*Scapular Muscles* (text-figs. 36–38):—I agree with Macalister (18) that the supraspinatus is larger than the infraspinatus in *Phascolomys* and the Phalangers, but I observed the reverse in *Phascolarctos*. Young (14) states that the infraspinatus is slightly larger than the supraspinatus. The subscapularis and teres major are essentially similar in all, and there is a certain amount of fusion between the latter and the latissimus dorsi and dorso-epitrochlearis. The teres minor is fascial in *Phascolomys*, thin and with a tendinous attachment to the scapula in *Phascolarctos*, and thin and muscular in *Phalanger* and *Pseudochirus*. Even when it is muscular there is a considerable degree of fusion with the infraspinatus. Meckel (6) states that the absence of a teres minor as a distinct muscle appears to be general amongst marsupials.

The characters of the *Coraco-brachialis* in many forms, including the animals described in this paper, have already been recorded, and Cunningham (2) has collected the observations. My own observations do not differ from his.

*Biceps*:—The two heads of origin are in contact, but not fused, in *Pseudochirus*, and the two bellies (gleno-ulnar and coraco-radial) are fused from the middle of the arm onwards. In the distal portion of the arm the two parts separate again and run to the radial tuberosity and coronoid. In *Phalanger* the tendons of origin are fused to form a tendinous sheet. The muscle bellies remain fused to the distal part of the arm where the stout radial and slender ulnar components are given off. In *Phascolomys* and *Phascolarctos* the origins are conjoined, but the bellies separate sooner from one another in the latter.

*Brachialis Anticus*:—In all forms it arises on the outer surface of the shaft of the humerus, and winds round it to be inserted into the ulna with, or deep to, the gleno-ulnar component of the biceps. In *Phascolarctos* it is fused with the biceps, but



it is separate from it in *Phascolomys* and the Phalangers. Macalister (18) showed that the conditions in *Phascolomys* are similar to those in many Polyprotodonts and Diprotodonts.

*Triceps* (text-figs. 36-38):—In *Phascolomys* I observed the long head arising from the lateral two-thirds of the axillary border of the scapula, and the humeral heads are indistinguishably fused. Macalister (8) stated that the long head arises from more than a third of the bone. In *Phascolarctos* the long head arises from a third of the axillary border of the scapula, and it passes to the distal third of the arm before it unites with the fused humeral heads. In *Phalanger* and *Pseudochirus* the long head also arises from a third of the axillary border, but it unites high up with the humeral heads.

*Anconeus*:—The anconeus internus, according to Cunningham (2), is generally present in the Marsupialia. In *Phascolomys*, *Phalanger*, and *Pseudochirus* it is a marked parallel-sided band running from the internal condyle to the olecranon, and the ulnar nerve passes under cover of it. In *Phascolarctos* it appears to be more continuous with the dorso-epitrochlearis. In *Phascolarctos* and *Phascolomys* it is not connected to a fibrous band which gives origin to the flexor carpi ulnaris. The anconeus externus is present in all forms, but it is least in *Phascolomys*, in which it has no connection with the triceps.

*Pronator Radii Teres*:—Cunningham (2) pointed out that this muscle has no coronoid head in the Marsupialia. The insertions vary. In my specimens the conditions are as follows:—

*Phascolarctos*: to middle two-fourths of the radial shaft.

*Phalanger*: to distal two-thirds of the radial shaft.

*Pseudochirus*: to distal two-thirds of the radial shaft.

*Phascolomys*: to distal half of the radial shaft.

*Flexor Carpi Radialis*:—This muscle is well developed. It exhibits a variable amount of fusion with the other members of the superficial flexor group, but the fusion is least in *Phascolarctos*. It is inserted into the base of the second metacarpal in *Phascolomys*, *Phalanger*, and *Pseudochirus*, but it runs to the third metacarpal in *Phascolarctos*.

*Palmaris Longus* is present in all. In *Phascolomys* Macalister (18) described a true palmaris longus and a palmaris accessorius, both arising from the internal condyle. In my specimen the accessorius does not arise from the condyle, but it is implanted into the side of the tendon of palmaris longus in the distal third of the forearm; and it has a very slender tendon which runs to the palmar pad. In *Phascolarctos*, *Phalanger*, and *Pseudochirus* there is no trace of the accessorius.

*Flexor Carpi Ulnaris*:—In all the animals described in the present paper the insertion is into the pisiform bone. But Macalister (18) described it as being attached to the fifth metacarpal in *Phascolomys*. Young (14) describes it as giving off



prolongations to the fifth metacarpal and the unciform in *Phascolarctos*.

*Flexor Sublimis Digitorum* :—This muscle is frequently strongly connected to the flexor profundus, and it is sometimes called the flexor perforatus because the profundus tendons pierce its tendons, which are very slender. The sublimis and profundus tendons separate out from the strong flexor mass in the distal part of the forearm.

*Pronator Quadratus* :—The extent of the interosseous space occupied by the pronator quadratus varies considerably. In *Phascolomys* I observed it extending over the distal half of the space, but Macalister says it is weak and only occupies the distal third. In *Phascolarctos* it occupies the lower fifth, but the extent is even less in *Phalanger* and *Pseudochirus*. Cunningham (2), however, described it as covering one third of the bones in *Cuscus* (*Phalangista maculata*).

*Supinator Longus* :—My observations on *Phascolarctos* differ in some respects from those of Macalister (5) and Young (14). It consists of two parts. The proximal division arises from the shaft of the humerus from close to the neck downwards, and it is thin and almost aponeurotic. The distal part, which is more muscular, arises from the lateral supracondylar ridge and by fibres which fuse with the extensors of the wrist. The two parts unite into a strong tendon which, passing under the abductor pollicis major, is inserted into the scapho-lunar bone. Young points out that it is both a radial flexor and supinator. It receives a slip from the deltoid. In *Phalanger* it is also large, but not divided into two parts. It springs from the proximal two-thirds of the lateral supracondylar ridge. No slip runs into it from the deltoid. These conditions are also present in *Pseudochirus*. The conditions in *Phascolomys* are, however, very different. It is thin and aponeurotic in parts, and it receives a strong band from the deltoid.

*Supinator Brevis* :—The extent of the radius embraced by this muscle varies. In *Phalanger* it covers less than the upper fifth, in *Phascolarctos* it covers the upper fifth, and in *Phascolomys* it envelops the upper two-thirds.

*Extensores Carpi Radiales* :—The existing records show that there is considerable variation in these muscles in the Marsupialia. In *Phascolomys* there is a single muscle arising from the external condyle and lateral ridge of the humerus and running to be inserted into the second and third metacarpal bones. But it is evident that the long and short extensors are combined in the single muscle. In *Phascolarctos* both long and short extensors are present and are inserted into the radial borders of the second and third metacarpals respectively. In *Phalanger* both muscles are present, but the brevior is a large and powerful muscle with three heads of origin as described by Cunningham (2).

*Extensor Communis Digitorum* :—In all forms it arises from the external condyle. In most Marsupialia it sends four tendons

to the four inner digits. But, as Young (14) mentions, and I observed myself, tendons go to each of the five digits in *Phascolarctos*.

*Extensor Secundus Digitorum*:—This muscle, which corresponds to the extensor minimi digiti of human anatomy, has been fully described in many Marsupialia by Cunningham (2), Young (14), and Macalister (5 & 18). In *Phascolarctos* it is in reality double. One muscle runs to the third digit as an extensor medius, and the other is inserted into the fourth and fifth digits. In *Phascalomys* and the Phalangers only the latter part is present.

*Extensor Carpi Ulnaris*:—In *Phascalomys* it arises from the external condyle of the humerus and upper part of the shaft of the ulna, and is inserted into the mesial border of the shaft of the fifth metacarpal bone. In *Phascolarctos* the ulnar origin head is similar to the above. But in *Phalanger* there is no ulnar head.

When a superficial view of the extensor muscles is taken in all the animals described in this paper, it is seen that intermuscular septa are well marked in *Phascolarctos*. In *Phascalomys* and the Phalangers there is more fusion of the bellies of the muscles.

*Extensor Ossis Metacarpi Pollicis*:—This muscle, as has already been pointed out by several authors, includes the extensor primi internodii pollicis. In *Phascalomys*, according to Macalister (18), it arises from the dorsum of the shaft of the ulna and the interosseous membrane, crosses the extensor carpi radialis tendon, and is inserted into the trapezium and thumb metacarpal. In *Phascolarctos* I observed it arising from the dorsum of the proximal third of the part of the ulna bordering the interosseous space, from the membrane, and from the greater part of the dorsum of the radius from the orbicular ligament distally. In *Phalanger* and *Pseudochirus* it also arises from both bones and the interosseous membrane, but the ulnar origin is lower and more extensive than in *Phascolarctos*, and the muscle belly gives off two tendons which wind over the extensor carpi radialis and supinator longus tendons.

*Extensor Secundi Internodii Pollicis*:—There is no trace of this muscle in *Phascolarctos*, and in this respect I agree with Young (14) and differ from Macalister (5), who stated that it is arranged as usual. In *Phascalomys* it runs from the lower third of the ulna to the last phalanx of the pollex. The tendon gave a short slip to the fascia over the metacarpo-phalangeal joint of the index. In *Phalanger* it also gives slips to the index and pollex, and Cunningham (2) describes two separate muscles in *Phalangista maculata*. It is therefore evident that the only extensor of the pollex in *Phascolarctos* is the additional tendon of the extensor communis digitorum; and in no other Marsupial is this arrangement present.

*Intrinsic Muscles of the Manus*:—The observations of Cunningham (2), Macalister (5, 18), Ruge and Young (14, 15) have given us a very complete account of the anatomy of these muscles. Young, in particular, has shown how they have become

modified in accordance with habits. He has also shown that the Koala is very different from the others, his conclusions being as follows:—"The digits form two groups, of which one, including the thumb and index finger, is opposable to the other, this latter comprising the three remaining digits. The index digit, in point of fact, constitutes a second thumb; and, in conformity with its unusual freedom of action, its special muscles are well developed. Moreover, as the result of the arrangement of the digits into two groups, the middle line of the hand no longer passes through the *third* digit, but along the *fourth*. The muscles of the hand are correspondingly modified, and hence, so far as regards their insertions, the arrangement is very different to what is ordinarily found."

*Muscles of the Posterior Extremities.*

*Gluteus Maximus*:—In *Phascolarctos* it has no origin from the iliac crest, but springs from the sacral and caudal vertebræ. The coarse fibres sweep over the great trochanter, thereby producing a rounded prominence; and are inserted into a considerable length of the femoral shaft. The fibres are continuous postero-mesially with the *lateralis caudæ*. In *Phascolomys* a broad, long agitator caudæ shuts off the gluteus maximus from the sacral and caudal vertebral spines, and a strong intermuscular septum, which gives origin to some of the fibres of both muscles, intervenes between them. The gluteus maximus also arises, as in all Marsupialia except the Koala, from the iliac crests posteriorly, and from the lumbar fascia. The whole muscle appears flattened, and it is inserted into the back part of the great trochanter. Cunningham (2) describes how the gluteus maximus is divided into three parts in *Phalangista maculata*, but there is no obvious separation into distinct parts in my specimen of *Phalanger orientalis*. There it is a long fan-shaped sheet composed of gluteus maximus, tensor fasciæ femoris, and agitator caudæ. It extends from the lumbar fascia anteriorly backwards along the iliac crest and spines of the sacral and anterior four caudal vertebræ. The part of the sheet representing the agitator caudæ has much coarser fibres than the other parts. The insertion of the sheet does not differ in any essential point from that in *Phalangista maculata*, already described by Cunningham. In *Pseudochirus* the conditions resemble those in *Phalanger*, but the fibres of the agitator caudæ are not so coarse, or so separate from the other parts of the muscle.

*Gluteus Medius*:—In all forms it is large, and frequently exceeds the maximus in size. In *Phascolarctos* it arises from the iliac crest, the gluteal surface of the ilium, and the sacral spines. It is inserted into the great trochanter. The fibres are in parts fused with the subjacent gluteus minimus, but there is no lamination as described by Young (14). In *Phascolomys* it is difficult to separate the medius and minimus. In *Phalanger* and *Pseudochirus* the medius and minimus are separate. The *Gluteus*

*Minimus* does not differ in any essential in the animals described in this paper except for the degree of adhesion to the medius. The *Gluteus Quartus* is present in all.

*Pyriformis*:—In all forms this is a strong triangular muscle arising from the side of the sacrum and running to the summit of the great trochanter of the femur. The *Obturator Externus* is likewise similar in all, and is large.

*Obturator Internus*:—This muscle is absent in *Phascolomys*, but present in all other forms. The *Gemelli* are present in all. They are both enormous in *Phalanger*, of moderate size in *Phascolarctos*, and the inferior one is large in *Phascolomys*.

The *Quadratus Femoris* is absent in *Phascolomys*. In *Phascolarctos* it arises entirely from the great sciatic ligament. In *Phalanger* it arises from the tuber ischii. The insertion is into the posterior border of the great trochanter.

*Sartorius*:—In the Marsupialia this muscle acts as an extensor, and an interval, filled with fascia, is present between its upper part and the quadriceps. It arises in all from the anterior superior iliac spine; and it is inserted into the inner side of the quadriceps tendon (*Phascolarctos*), or the inner aspect of the patella and knee-joint (*Phalanger*, *Pseudochirus*, *Phascolomys*).

*Quadriceps Extensor*:—The rectus femoris has only the straight head in *Phascolomys*, but both heads are present in *Phascolarctos*, *Pseudochirus*, and *Phalanger*. In the other elements these animals are all essentially similar, and the vastus externus component is large. The tendon is inserted in all into the tibia. It contains a cartilaginous patella in *Phascolomys*, *Phalanger*, and *Pseudochirus*, but none in *Phascolarctos*. Waterhouse (17) stated that *Phascolomys* also has no patella, and used this character among others to show that they are related. As many observers have recorded the presence of the patella in the Wombat, it is evident that this is not a character linking it to the Koala, as Waterhouse believed.

*Gracilis*:—When the skin is removed it is seen that the muscles on the mesial aspect of the thigh are concealed by the gracilis to a variable extent. It arises from the symphysis pubis and a variable extent of the descending ramus, and from the mesial extremity of the marsupial bone. It is inserted into the proximal half of the mesial border of the shaft of the tibia. In *Phascolomys*, *Phalanger*, and *Pseudochirus* it goes to the proximal half of the tibia, but in *Phascolarctos* it only runs to the proximal third.

*Biceps Cruris*:—In *Phascolarctos* the biceps and semimembranosus have a strong, common tendon of origin from the ischial tuberosity and caudal vertebrae. The biceps is thin and triangular, and inserted into the fascia over the proximal two-thirds of the fibula. No femoral component enters into the biceps. Young (14) points out that the nature and extent of the insertion are associated with the semi-flexed attitude of the limb. In *Phalanger* the muscle arises from the ischial tuberosity, along with semi-



membranosus, and from the caudal vertebræ, the two parts being separate. No femoral head is present. The ischial part expands and becomes fan-shaped; it is inserted into the fascia over the fibula in the proximal two-thirds of the leg. The caudal part is at first superficial to the ischial part, but winds round it and divides into two portions. One of these fuses with the ischial part. The other fuses with semitendinosus, and then is inserted into the middle of the subcutaneous mesial surface of the tibia. The conditions present differ in several respects from Cunningham's account of the muscle in *Phalangista maculata*. In *Pseudochirus* the conditions are essentially similar to those in *Phalanger*. In *Phascolomys* it arises entirely from the ischial tuberosity along with semimembranosus, and it is inserted into the fascia over the proximal third of the fibula, and into the bone itself, but it is not divisible into two parts as in the *Phalangeridæ*. No femoral head is present. Its insertion is less than in *Phascolarctos* and the *Phalangeridæ*.

No bicipiti accessorius is present in any of these animals.

*Semimembranosus* (text-fig. 40):—In all forms it is muscular from origin to insertion, and there is a variable amount of union to the biceps; and the course in all is from the tuber ischii to the mesial aspect of the leg. In *Phascolarctos* it is inserted into the quadriceps tendon, internal tuberosity of the tibia, and the fascia of the leg; and some of the fibres fuse with the triceps adductor femoris. In *Phalanger* the insertion is moved farther distally. It avoids the adductor and quadriceps, passes under the internal lateral ligament of the knee, and is attached to the anterior tuberosity of the tibia. And, as Cunningham (2) pointed out in *Phalangista maculata*, it must rotate the leg on the thigh and act as a powerful flexor. In *Phascolomys* it is inserted into the mesial aspect of the head of the tibia.

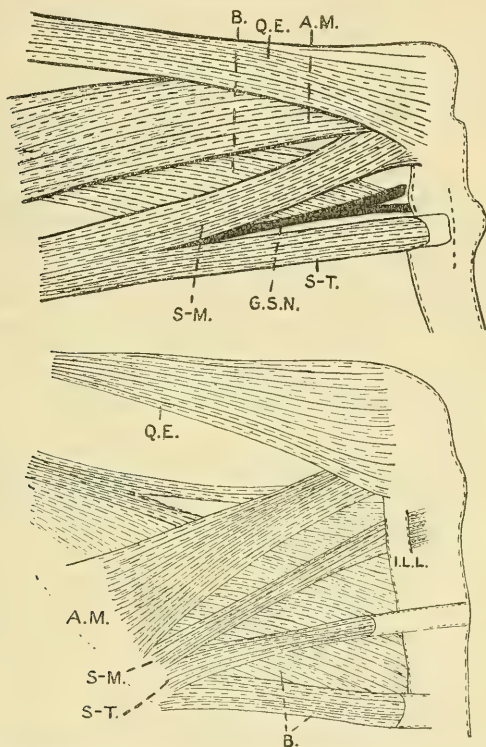
*Semitendinosus* (text-fig. 40):—In *Phalanger* it is inserted into a narrow strip of the middle of the ventral border of the shaft of the tibia. But Cunningham (2) described it as going to the mesial surface of the bone in *Phalangista maculata*. In *Phascolarctos* it is inserted into the mesial aspect of the tibia at the level of the prominent tubercle on the anterior (ventral) border. In *Phascolomys* it runs to the mesial border of the tibia in its middle third. No tendinous inscription is present in any of these Marsupialia. The muscle fuses with the biceps in *Phalanger* and *Phascolomys*, but is quite free in *Phascolarctos*. But Macalister (18) described it as free from other muscles in *Phascolomys* and *Phalanger*.

*Gastrocnemius*:—In *Phalanger*, as in *Phalangista maculata*, the two parts from origin to insertion are quite separate. The inner head arises from the back of the internal condyle of the femur, and its tendon is inserted into the tuberosity of the os calcis. The outer head arises from the proximal sixth of the shaft of the fibula and from the intermuscular membrane between it and the peronei; its tendon is inserted into the tuberosity of the



os calcis deep to that of the mesial part of the muscle. Only a thin membrane connects the two parts. In *Phascolarctos* the two parts arise as in *Phalanger*; at the junction of the proximal and middle thirds of the leg a strong, narrow aponeurosis, which ultimately forms the tendo Achillis, begins to appear on the outer part of the muscle, and the inner part is attached to it. In

Text-figure 40.



Adductor and hamstring muscles of *Phascolarctos cinereus* (above), and *Phalanger orientalis* (below).

A.M.: adductors; B.: biceps; G.S.N.: great sciatic nerve; I.L.L.: internal lateral ligament of knee; Q.E.: quadriceps extensor; S-M.: semi-membranosus; S-T.: semi-tendinosus.

*Pseudochirus* the two parts unite, so it resembles that in *Phascolarctos* rather than *Phalanger*. In *Phascalomys* the inner head arises from the back of the internal condyle, and from a small piece of the popliteal surface of the femur on both mesial and lateral aspects. The outer head arises from the sesamoid bone at the back of the external condyle. Both remain separate for a considerable distance, the mesial part overlapping the lateral one,

But they are inserted into a tendo Achillis. It is therefore evident that the degree of separation of the internus and externus differs in these Marsupialia.

*Soleus*:—In *Phascolarctos* and *Phalanger* there is no separate soleus, and the observations of Cunningham (2), Macalister (5), and Young (14) have shown that it is really contained within the gastrocnemius externus, as the latter has a fibular origin. Moreover, the plantaris lies under cover of the inner part of gastrocnemius externus, and not under the part which corresponds to soleus. In *Phascolomys* the soleus has a small fibular head, but no tibial origin.

*Plantaris*:—In *Phalanger* and *Phascolarctos* it is well developed, and it is inserted into the plantar fascia, but Young (14) observed it inserting into the tendo Achillis in one Koala. In *Phascolomys* it is absent.

*Tibialis Anticus*:—In all forms it arises from the outer surface of the shaft of the tibia, and the interosseous membrane; but its insertion varies. In *Phascolomys*, according to Macalister (18), it is inserted into the entocuneiform. In my specimen two tendons are given off. One goes to the entocuneiform, and the other to the hallux. The latter takes the place of the extensor longus hallucis, which is absent as a separate muscle in my specimen. In *Phalanger* and *Phascolarctos* the insertion is into the entocuneiform alone. And in these genera a separate extensor hallucis arises from the fibula.

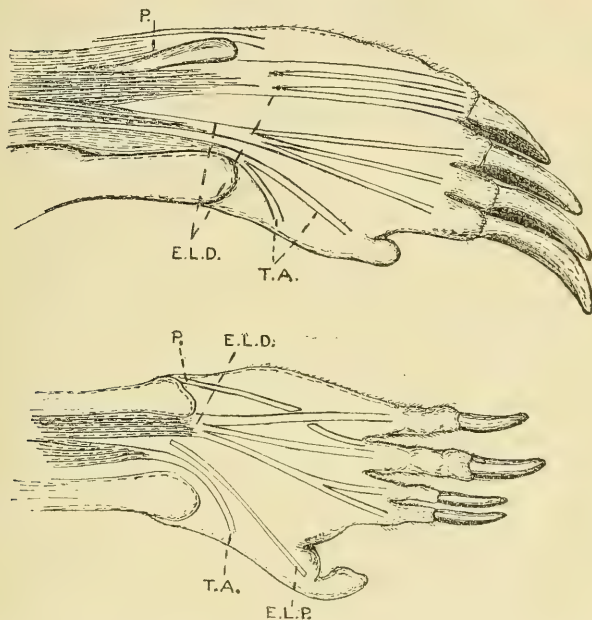
*Extensor Digitorum Longus*:—Macalister (18) describes it in *Phascolomys* as arising from the fibula and front of the tibia, and running to the four toes. In my specimen (text-fig. 41) it arises from the tibia, fibula, and interosseous membrane. It soon divides into slender inner and stout outer portions. The former gives three delicate tendons to the first, second, and third toes, but the three stout tendons of the lateral portion go to the inner, dorsal, and lateral parts of the inner toe. In *Phascolarctos* (text-fig. 41) the muscle likewise consists of two parts, whereas Young (14) states that in being separable into two portions the Koala differs from such marsupials as have been examined. Three tendons emerge. The first is slender and divides into slips for index and medius. The second is of medium size and runs to annularis. The third is powerful and divides into tendons to annularis and minimus. In *Phalanger* three tendons are disposed as in *Phascolarctos*, but the muscle itself is not divisible into two. There is, therefore, a greater resemblance between these arboreal forms than there is between *Phascolarctos* and *Phascolomys*.

*Peronei*:—The muscles composing the groups differ considerably. In *Phascolarctos*, as pointed out by Young (14), there are four components—longus, brevis, quarti metatarsi, and quinti metatarsi,—and all are fibular in origin. In *Phalanger*, as in *Phalangista maculata*, there are three components—longus, brevis, and some muscular slips representing portions of the extensor brevis digitorum. In *Phascolomys* Macalister (18) described long and

short peronei and an accessory quinti tendon detached from the last for the first phalanx of the outer toe. In my specimen this last slip is absent, but I believe it is represented by one of the slips of the extensor longus digitorum.

Ruge pointed out that the *extensor brevis digitorum* was originally derived from the peroneal group of muscles. It is present in all Marsupialia, but varies in the degree of development. In *Phalanger* it runs to the four toes. In *Phascolarctos* it is

Text-figure 41.



Extensors of foot in *Phascolomys mitchelli* (above) and *Phascolarctos cinereus* (below).

E.L.D.: extensor longus digitorum; E.L.P.: extensor longus hallucis; P: peronei; T.A.: tibialis anticus.

inserted into the two inner toes. And in both forms it arises from the fibula. In *Phascolomys* it arises from the outer part of the tarsus, and is inserted into the inner pair of toes.

*Tibialis Posticus*:—This muscle has already been fully described by Cunningham (2), Young (14), and Macalister (5, 18). In *Phascolomys* it is a single muscle arising from the back of the tibia and running to the inner part of the scaphoid. In *Phascolarctos*, *Phalanger*, and *Pseudochirus* it is double. In the Koala two fibular slips run to the scaphoid and entocuneiform; but in the Phalangers both tibial and fibular bellies run to the scaphoid.

The *flexor longus digitorum* includes flexor longus hallucis, and arises from tibia and fibula. Superficial and deep tendons are present, and the latter pierce the former, as in the manus.

The *popliteus* occupies practically the whole interosseous space.

The intrinsic muscles of the pes have already been fully described (2), and the mid line in *Phascolarctos* has been moved, as in the case of the manus, with resulting modifications in structure.

### *Summary of Myological Features.*

1. In all animals described in this paper there are traces of adherence to the primitive lamination which characterises the development of mammalian muscles in general. In *Phalanger*, *Pseudochirus*, and *Phascolomys* we observe:—1. Inseparability of the prevertebral muscles; 2. Undivided state of the rhomboideus; 3. Fusion of the trapezius with the pectoral fascia and clavicular deltoid; 4. Biceps flexor cruris has only one head of origin; 5. Separate character of the hamstrings; 6. Degrees of separation of levator scapulæ and serratus magnus. In *Phascolarctos* the following additional ones are present:—7. Platysma continuous with muscles of orbit, auricle, and mouth; 8. Sterno-hyoid prolonged to mandible; 9. Styloid muscles a single sheet; 10. Digastric and mylo-hyoid fused; 11. Hyoglossus transverse and not attached to hyoid; 12. Omo-hyoid passes into tongue; 13. Internal oblique has tendinous intersections; 14. Quadratus lumborum absent; 15. Supinator longus very long; 16. Pronator quadratus small; 17. Coraco-brachialis double; 18. No extensor secundi internodii pollicis; 19. Origin of gluteus maximus; 20. No soleus; 21. Tibialis posticus double; 22. Characters of peronei; 23. Intrinsic muscles of manus and pes.

2. Many of the myological features are similar in all these animals, in many other Marsupials, and in animals belonging to the other Mammalian orders.

3. Most of the characters not included in the above groups are adaptations to suit modes of life.

4. In the small group of characters—omo-trachelian and deltoid—not included in the three preceding groups, the Koala and Wombat differ from the Phalangers.

### CLASSIFICATION.

All zoologists have separated *Phascolomys* from the Phalangeridæ, so the work of the systematist is limited to fixing the proper position for *Phascolarctos*. To do so it is necessary to examine all characters, both external and internal. The large assemblage of data so obtained must then be reduced by excluding characters of little or no value for purposes of classification. In the first place, one must remove those which are varying degrees of persistence of primitive conditions which were once present in their common ancestor. Secondly, structures which are similar as



the result of convergence must be excluded as they are not evidence of affinity. Thirdly, those features which are common to all the animals under consideration, to many other Marsupials, and to other Mammals cannot be employed in making a classification of the Wombat, Koala, and Phalangers. We are then left with a series of useful characters, and those which are sheltered deep down in the body should be of value, for they are less liable to be influenced by climate and habits than are the more superficial characters.

The anatomical characters must be arranged in four groups:—

A. Those in which *Phascolarctos* and *Phascolomys* differ from the Phalangeridæ. They support the systems of Weber (12) and Winge (13), and Weber's family of Phascolarctidæ is employed here for the Koala and Wombat.

B. Those in which *Phascolarctos* and the Phalangeridæ differ from *Phascolomys*. Special attention must also be paid to the comparison between *Phascolarctos* and *Pseudochirus*. These support the systems of Thomas (11), Bensley (1), and Gregory (4).

C. Characters in which *Phascolarctos* differs from *Phascolomys* and the Phalangeridæ.

D. Characters differing in all forms.

Groups C and D are evidence in favour of Pocock's system.

In estimating the value of the anatomical data one must always bear in mind the habits and the character of the diet of these animals. *Phascolarctos* and the Phalangeridæ are arboreal animals, but lead different kinds of life. The latter are active, but the former is a clumsy, sluggish creature, clinging to branches by its modified feet. *Phascolomys*, on the other hand, is an active animal. Its hind-limbs are fossorial and its fore-limbs are for active progression. A study of the myology shows that these modes of life are accompanied by numerous differences in the muscles. As regards the diet, that of *Phascolarctos* and *Phascolomys* is bulky, whereas that of the Phalangeridæ is not; and the Phascolarctidæ have specialisations in the structure of their alimentary canal to meet the demands imposed by it. Finally, although the life habits differ, we find the arboreal sluggish Koala and the active fossorial Wombat possess numerous characters of great importance in their skeletons and soft parts, in which they differ from the active arboreal Phalangeridæ. We must always aim at discovering the part played by each structure in the animal economy before we can assess its true systematic value. Some characters are well understood, but there are others of whose general adaptive purpose we are totally ignorant.

A. *Characters in which the Phascolarctidæ differ from the Phalangeridæ.*

*External Characters:*—Pocock (9) showed that the supratragus in the Phalangers and many other Mammals is a prominent ridge with a well-developed lobe; but it is low, inconspicuous, and



devoid of lobate thickening in the Phascolarctidæ. This, in my opinion, is a character of importance, for it does not appear to depend on modes of life. Pocock has also shown how the various genera can be separated by the auricular characters. As regards the mammae the Phascolarctidæ have only two, but the Phalangeridæ have four. Pocock found two only in *Trichosurus*. The tail is a well-developed organ in the Phalangeridæ, and rudimentary but muscular in the Phascolarctidæ; probably the reduction is the result of life habits. The Koala clings only by its hands and feet to the branches, so the tail would be useless; and a tail would be in reality an impediment to the Wombat. The Phalangeridæ have vibrissæ on the wrist and hind foot, but no traces of these tactile hairs are present in the Phascolarctidæ. Moreover, the integuments of the hind feet differ. In the Phalangeridæ the skin is striated over the well-marked pads, but it is granular on the reduced pads in the Phascolarctidæ.

*Myology*:—In the Phascolarctidæ there is no cleido-occipital, the omo-trachelian is single, and the unbroken deltoid gives a slip to the forearm. In the Phalangeridæ, on the other hand, the cleido-occipital is present, the omo-trachelian is double, and the deltoid, which is in two parts, does not give a slip to the forearm. Although these are prominent differences, they are of very minor importance in classification.

*Circulatory System*:—In the Phascolarctidæ the pericardium adheres to the diaphragm, the post-caval vein does not conceal the abdominal aorta, and anterior jugular veins are absent. In the Phalangeridæ the pericardium is connected to the diaphragm by two membranous sheets, and the post-caval vein conceals the posterior part of the abdominal aorta. I found anterior jugular veins in *Trichosurus* and *Phalanger*, but not in *Pseudochirus*; perhaps they exist in the latter, for my specimens had been preserved so long in spirit that the veins, if present, had shrunk to minute proportions.

*Alimentary Canal*:—Cheek-pouches are absent in the Phalangeridæ, but present in the Phascolarctidæ; they are well-marked in *Phascolarctos*, but rudimentary in *Phascolomys*. I believe, however, that these diverticula are, in reality, adaptive in function. The stomach is simple in both families, but possesses the so-called gastric gland in the Phascolarctidæ. That structure has been regarded by many zoologists as of special value for showing the close relationship between *Phascolarctos* and *Phascolomys*. Indeed, Forbes (3) regarded it as the main test. But Johnstone (16) showed that it is no special gland; it is an evagination and folding of the mucous membrane plus an extension of the normal gastric glands. It is in reality a means of increasing the secreting area of the stomach to fulfil the demands imposed by a bulky diet. The Phalangers do not consume a bulky diet, so cheek-pouches are absent, and there is no trace of the gland patch. Unless there were other characters showing a close relationship between

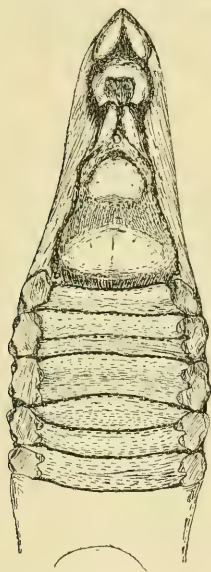
*Phascolarctos* and *Phascolomys* the gland patch alone could not be employed as a test of affinity.

The liver also possesses distinguishing characters. In the *Phalangeridæ* the caudate lobe is present, but the main lobes are not complicated by secondary sulci. In the *Phascolarctidæ*, on the other hand, there is no caudate lobe, and many secondary sulci subdivide the main lobes.

*Phascolarctos* predominates over *Phascolomys* in the size of the cheek-pouches, the complexity of the gland patch, the subdivision of the main hepatic lobes, and the length of the gall-bladder.

As regards the dentition, Waterhouse (17) pointed out long ago

Text-figure 42.



The hard palate in *Phascolomys mitchelli*.\*

that "the approximation to the Rodent-like dentition which is exhibited by the Wombat is perceptible in the Koala, in the smaller development of the posterior incisors and canines of the upper jaw, and the total absence of those premolars which, in the typical *Phalangers*, intervene between the canine and the five molars of the upper jaw, and the incisor and corresponding teeth in the lower jaw." Bensley (1) has shown, however, that the dental characters which would point to a resemblance between *Phascolarctos* and *Phascolomys* are probably due to convergent evolution, and Forbes (3) rightly considered that the dental characters in *Phascolomys* are adaptive in

\* Compare with Plate V in my paper on the Koala (10).

character. Tomes (19) showed that the dental enamel in *Phascolomys* possesses histological characters which separate it from most, if not all Marsupialia, but he did not specifically mention *Phascolarctos*. It appears, therefore, that in the dentition we have an assemblage of characters brought about by adaptation and convergence, so they cannot be used to show a close affinity between the Koala and Wombat.

*Generative Organs and Development*:—In the Phascolarctidæ the vaginal culs-de-sac are separate, but they coalesce in some of the Phalangeridæ, at least in *Trichosurus* (Forbes). As regards the fetal membranes, Professor J. P. Hill informs me that they are fundamentally the same, but differing in details, in the Koala and Wombat. Moreover, the conditions in the Phascolarctidæ differ entirely from those in the Phalangeridæ.

*Osteology*:—I have compared the conditions in the material at my disposal with Owen's account (8), and the essential points are shown in the subjoined table:—

Phascolarctidæ.	Phalangeridæ.
1. Pterygoid processes large.	1. Processes small.
2. Intermaxillary bones increased transversely.	2. Bones not increased transversely.
3. Palatal process of maxilla forms a considerable part of boundary of incisive foramina.	3. Maxillæ form a small part of boundary.
4. Palatal foramina entirely on palate bones.	4. Palatal foramina extend into maxillæ.
5. Groove obsolete.	5. Groove runs from foramen rotundum to Gasserian fissure.
6. Not ossified.	6. Margin of tentorium ossified.
7. Mid spongy bone simple*.	7. Convolutions of mid spongy bone numerous and delicate.
8. Halves of mandible united.	8. Halves separate.
9. Seventh cervical vertebra perforated.	9. Not perforated.
10. Process beneath the sixth cervical process short.	10. Process greatly expanded.
11. Anterior arch of the atlas partly cartilaginous.	11. Arch entirely osseous.

In many of the osteological characters not included in the above list there are differences in degree only in the Phalangiers, *Phascolarctos*, and *Phascolomys*. Doran has shown that the ear ossicles of *Phascolarctos* differ entirely from those in the Phalangeridæ, but they have some points in common with those of *Phascolomys*.

*B. Characters in which Phascolarctos and the Phalangeridæ differ from Phascolomys.*

*External Characters*:—In *Phascolomys* flaps of skin from the lower lip protrude into the diastemata, but this is a new development, associated, as in many Rodentia, with the type of dentition. There is, however, no trace of these in the other animals. As

\* Owen's account is relied on here as the skulls in my possession are not perfect as regards the turbinate bones.

regards the manus and pes, it is necessary to consider both the external appearances and the internal structure. Pocock (9) and others have already described the external appearances, and the following conclusions can be drawn from their accounts:—

1. The fore foot possesses no special modifications in *Trichosurus*.

2. The conditions in *Phascolomys*, which are adapted for a fossorial and ambulant life, have some resemblance to those of *Trichosurus*, but differ in many ways from those in *Phascolarctos* and the Phalangeridæ. Among these are the length of the digits, the shortness and bluntness of the claws; and there is no division of the digits into two opposing groups. The pads are reduced.

3. In *Phascolarctos* and the Phalangeridæ the pollex and index can be opposed to the long axis of the manus, and Young regarded these two digits as constituting one group, the remaining three digits forming a second. These conditions are slightest in *Phalanger*, intermediate in *Pseudochirus*, and most highly developed in *Phascolarctos*. The latter differs from all Phalangers, except *Trichosurus*, in the appearance of the pads. In *Phalanger* and *Pseudochirus* the pads are striated, but they are granular in *Phascolarctos* and *Phascolomys*. Moreover, myological literature shows that *Phascolarctos* is peculiar in many ways. I agree with Pocock's scheme, which shows that the characters of the manus in *Phascolomys* differ from those in the other animals. And although the others have features in common, there are sufficient characters to distinguish *Phascolarctos* from the Phalangeridæ.

Bensley (1) described and figured the pes of the Diprotodonts, and drew important conclusions as regards the affinities of the animals. He pointed out that the pes in *Dromicia* is prototypal for the Phalangeridæ, and those of *Phalanger* and *Pseudochirus* conform more or less closely to it. But the conditions in *Phascolarctos* show no close relation to those in *Pseudochirus*. The general conformation of the digits is the same, but the pads are all reduced, the sole being covered with soft, granular skin as in *Phascolomys*. The hallux is much farther back than in *Pseudochirus*, so it is more perfectly opposable. A slightly greater displacement would put its axis in line with that of the fourth digit, which it opposes. The foot differs in *Phascolarctos* and *Phascolomys* both in external appearance and internal structure.

Although the pes of *Phascolarctos* differs from that in *Pseudochirus* the dental characters are similar, but reach a higher degree of development in the former. Bensley (1) showed that these genera have quadrituberculate molars with selenoid cusps. The upper teeth have reduced external styles, with or without intermediate conules. In *Phalanger* and *Trichosurus* the quadrituberculate molars have bunoid cusps. And the upper teeth have neither external styles nor intermediate cusps. Moreover, as



shown on page 889, there are some resemblances between the teeth of *Phascolarctos* and *Phascolomys* which have resulted from convergence. These, however, must be excluded for purpose of classification.

*Osteology* :—The contrast in the skeletal characters are tabulated as follows :—

<i>Phascolarctos</i> and the <i>Phalangeridæ</i> .	<i>Phascolomys</i> .
1. Zygoma extended vertically and has no twist.	1. Zygoma has a marked twist.
2. Elements of occipital bone confluent.	2. Elements not all confluent in many skulls, but not in all.
3. Characters of supra-occipital.	4. Processes from petro-mastoid.
4. Occipital processes arise from ex-occipital.	5. Bulla from temporal bone.
5. Bulla from alisphenoid.	6. Pit obsolete.
6. Petrous has a large cerebellar pit.	7. Four pieces in sternum.
7. Six pieces in sternum.	9. Third trochanter present.
8. Characters of humerus.	
9. No third trochanter on femur.	

*Myology* :—*Phascolomys* differs from the *Phalangeridæ* and *Phascolarctos* in the absence of the quadratus femoris, obturator internus and popliteus, and in having only one head to the rectus femoris.

*Circulatory System* :—*Phascolomys* has no trace of a vena transversa (text-fig. 32).

It is necessary to remark on the comparison between *Phascolarctos* and *Pseudochirus*, because these have been placed close together in systems of classification. In a detailed examination of their anatomy one finds they differ from other *Phalangers* and *Phascolomys* in the character of the teeth and straightening out of the inflected angles of the mandible. As regards the visceral anatomy and myology, there is no way in which they can be marked out from other forms. I can see no reason other than the condition of the teeth and mandible for separating *Pseudochirus* from the other *Phalangers*, but I consider these alone as sufficiently important to do so.

When the characters mentioned in groups A and B are reduced by the elimination of the unimportant ones the following lists are obtained :—

A. Characters separating the *Phascolaretidæ* from the *Phalangeridæ* :—

1. Supratragus, tarsal vibrissæ, skin of pads and tail.
2. Gastric gland patch and liver.
3. Foetal membranes.
4. Position of palatal foramina.
5. Characters of symphysis menti.
6. Characters of the mid-turbinal bone (Owen).
7. Characters of the ear ossicles.



B. Characters separating *Phascolomys* from *Phascolarctos* and the *Phalangeridæ* :—

1. Formation of the alisphenoid bulla.
2. Site of occipital processes.
3. Pieces in sternum.
4. Third trochanter of femur.
5. Dentition.
6. Some of the characters of manus and pes.

C. *Characters in which Phascolarctos differs from the Phalangers and Phascolomys.*

*External Characters* :—Pocock (9) showed that there is a rhinarium in *Phascolomys* and the *Phalangeridæ*, but no true rhinarium is present in *Phascolarctos*; and the nostrils of the latter are also peculiar. In the same paper he deals with the characters of the marsupium, and points out that *Phascolomys* is intermediate between the *Phalangeridæ* and *Phascolarctos*. Moreover, the pouch of the latter is not closely related to that of any genus of the *Phalangeridæ*.

*Myology* :—In the summary of myological features at the end of the first part of this paper I enumerated many conditions representing adherence to the primitive lamination of the muscles. But these cannot be used for purposes of classification.

The other points are given in the following table :—

<i>Phascolarctos.</i>	<i>Phascolomys</i> and <i>Phalangeridæ.</i>
1. Occipital crest curves backwards.	1. Not so.
2. Alisphenoid bullæ as long as occipital processes.	2. Not so in <i>Phalangers</i> . Bulla temporal in <i>Phascolomys</i> .
3. Characters of nasal bones.	
4. Anterior margin of septum nasi concave.	4. Convex.
5. First dorsal spine scarcely exceeds seventh cervical.	
6. No patella.	6. Patella thin and cartilaginous.
7. Vagina musculina present.	7. Absent.
8. No azygos lobe.	8. Right lung has azygos lobe.
9. Epiglottis entire and far from tongue.	9. Epiglottis notched and close to tongue.
10. No faucial tonsil.	10. Fauical tonsils present.
11. Thick ureteric venous plexus.	11. Absent.

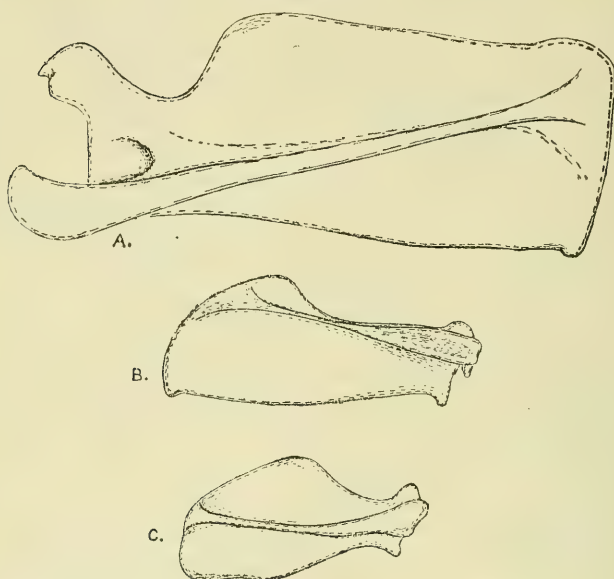
D. *Characters differing in all forms.*

In the first part of this paper I described no fewer than thirty-two myological features differing in all forms. But these fall into primitive and adaptive groups, and are useless for purposes of classification. As regards visceral anatomy, there are many points differing in all forms. Some of these are undoubtedly

adaptive, but others cannot be included in that category. The visceral and osteological characters are tabulated as follows:—

1. Oral vestibule, palatal formula, tongue.
2. Spleen, thymus, cervical lymph-glands.
3. Division of the right auricular appendix.
4. Branches of the aortic arch.
5. Number of dorsal vertebræ, ribs, intercostal soft parts.
6. Relative length of facial part of skull.
7. Characters of glenoid cavity.
8. Size and perforations of lachrymal bone.
9. Characters of scapula.

Text-figure 43.



The scapula in *Phascalomys mitchelli* (A.); *Phascalartos cinereus* (B.); and *Phalanger orientalis* (C.).

### Conclusions.

From an examination of these four groups of characters I have come to the following conclusion:—

1. *Phascalartos* cannot be included in the *Phalangeridæ*. Although dentition and foot structure have led some observers to put it in that family in close relation to *Pseudochirus*, there are many very important points in which it differs from them. If they are united it will be by superficial characters, and one will

break up the series of fundamental characters uniting the Koala and Wombat.

2. *Phascolarctos* is united to *Phascolomys* by characters whose importance far outweighs the resemblances between the former and the Phalangeridæ. The major ones enumerated on page 892 are regarded as of value by anatomists and evolutionists.

3. The characters peculiar to *Phascolarctos* are not sufficiently important to place it in a separate family. But they are useful for distinguishing it from *Phascolomys* in the family Phascolaretidæ.

4. I agree with Weber and Winge that there should be only two families, one for the Phalangers, and one for the Koala and Wombat; and there are characters of sufficient importance to place each of the animals in the latter in a separate subfamily. My views are tabulated thus:—

Family PHASCOLARCTIDÆ.

Subfamily 1. PHASCOLARCTINÆ.

2. PHASCOLOMYINÆ.

Family PHALANGERIDÆ.

Subfamily 1. PHALANGERINÆ.

*Phalanger*, *Trichosurus*.

Subfamily 2. PSEUDOCHIRINÆ.

*Pseudochirus*.

5. If one simply enumerates characters and strikes a balance he will obtain one form of classification, but if he considers each feature and tries to detect the part it plays in the animal œconomy his results will be quite different. They will lead him to place the Koala and Wombat in the same family.

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39. Experimental Evidence that Commensalism may be beneficial to Crustacea. By EDWARD B. POULTON, D.Sc., F.R.S., F.Z.S., Hope Professor of Zoology and Fellow of Jesus College in the University of Oxford.

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The special associations of Crustacea with organisms believed to be disliked by their enemies—with Sponges, Ascidians, and Sea-anemones—has probably been derived from a more generalized use of animal and vegetable growths for the purpose of concealment. The following experiments proved that two conspicuously coloured forms associated with Hermit-crabs were intensely distasteful to fishes, and that one of the crabs, when deprived of its associate, was greedily devoured. The experiments were carried out, with the help and advice of Prof. W. Garstang, in the Marine Biological Laboratory at Plymouth in the summer of 1890. The results have often been described, but never published.

(1) *Pagurus bernhardus* and its Sea-anemone, *Sagartia parasitica*.—These Crustacea were commonly dredged up at Plymouth, and large specimens bore on the shells—generally whelks—from two as to as many as six of these large brightly coloured actinians. Prof. Garstang had already obtained much indirect evidence of the value of the association, for he had often found the young Hermit-crabs, too small to carry a Sea-anemone, in the stomach of gurnards and other fishes. They had been swallowed entire, their borrowed shells and all. He had, however, never found in the fishes any of the larger crabs living in shells suited for carrying *Sagartia*\*.

I first tested the nematocysts of the *Sagartia* by touching it with the tip of my tongue, and at once experienced a sharp smart which endured for many hours. Pieces of about the size and shape of the bits of meat on which the fish in one of the tanks were accustomed to be fed were then cut from a Sea-anemone and thrown into the tank. Misled by this, a few fishes seized pieces of the *Sagartia*; but no sooner had one been received into the mouth, than it was shot out again with much force, and the fish shook its head violently from side to side, apparently feeling the same smart which I had experienced myself. After these first trials not one of the fish would touch the pieces, and it was obvious that the great majority saved themselves by yielding to the stimulus provided by the behaviour of the others.

(2) *Pagurus cuanensis* and the Sponge, *Suberites domuncula*.—This small Hermit-crab, also common at Plymouth, inhabits a cavity in the sponge, the tip of its tail being fixed in a small

\* These facts are recorded in "Colours of Animals," Internat. Sci. Ser., Lond. 1890, p. 203.



gastropod shell, while the rest of its body lies in a spiral canal continuous with that of the shell and gradually prolonged from it with the growth of the two associated organisms. The small shell was evidently inhabited by the young crab when the association began, but had become deeply buried in the sponge at the time when the experiments were made. The sponge was of the usual orange-red colour, although they are sometimes dark and comparatively inconspicuous. In size and shape it resembled a smallish potato.

When disturbed or frightened in any way, the crab darted back into its sponge exactly as other Hermits dash into their shells.

In order to obtain pictures of this species and *P. bernhardus* under as natural conditions as possible, the objects dredged up with each species were arranged in a dish, which was lowered into an aquarium so that its edge was in contact with the glass front and its contents well lighted from above. The crabs were secured in the most convenient position by tying to a stone in the dish. Although the string was wound so as not to touch *P. cuanensis*, and was, in fact, separated from its body by a considerable thickness of sponge, the crab quite understood the situation, and spent the whole time the artist was at work in trying to wear through the string with its two large claws. Thus occupied and stretching out of its canal, it was an admirable sitter.

Prof. Garstang had already recorded that sponges as a group are intensely disliked by fishes\*, but I was anxious to test this special example and compare its palatability with that of the crab. Pieces like those of the *Sagartia* were therefore thrown into the aquarium, but were recognized as unpalatable even more quickly than the others, and seized by fewer fishes. When taken they were instantly rejected. The *Pagurus* was then offered deprived of his sponge; there was a wild struggle, and the fortunate captor swallowed him in a moment.

It was evident that both these Hermit-crabs are associated with organisms possessing qualities rendering them unpleasant to fishes—qualities advertised by conspicuous warning colours. One of the crabs was shown on this occasion to be very palatable to fishes, and the other previously by Prof. Garstang, to be much sought after by them. Although the experiments described were very few, the results were so definite and clear that there can be little doubt about the meaning of the association in these and other similar examples of commensalism in Crustacea.

The beautiful illustrations, projected upon the screen, were painted in 1890 by my friend the late Mr. H. M. J. Underhill, of Oxford, who has reproduced the appearance of the living animals in their natural surroundings with wonderful skill.

\* "Colours of Animals," l. c.

40. Description of a New Lizard of the genus *Chalcides*, from the Gambia, living in the Society's Gardens.  
By E. G. BOULENGER, F.Z.S. (Curator of Reptiles).

[Received October 5, 1922 : Read November 7, 1922.]

The Society recently received from H.E. Capt. C. H. Armitage, C.M.G., a generous donor to its collection, a number of reptiles from the Gambia. Among these was a Lizard of the genus *Chalcides* which is evidently undescribed, and for which I propose the name of *Chalcides armitagei*, after its discoverer.

*CHALCIDES ARMITAGEI*, sp. n.

Snout more conical than wedge-shaped, but with distinctly projecting labial edge. Eye small. Ear-openings not larger than the nostril, on a line with the mouth. Nostril pierced mostly in advance of the suture between the rostral and the first labial. Supranasals united. Frontal longer than broad. Fourth labial entering orbit. Body very elongate. Sides of body not distinctly angular. Scales perfectly smooth, in 24 rows round the middle of the body. Limbs short tridactyle. Length of hind-limb not quite equal to distance between eye and fore-limb. Fore-limb equals in length distance between posterior border of orbit and snout. Tail shorter than head and body.

From snout to vent 119 millim.; tail 82 mm.

Great variation is to be found in the structure of the Lizards of the genus *Chalcides*, especially in the proportions of the limbs and body, and in the number of digits, where we find all stages of degeneracy, there being species with five, four, three, or even two fingers or toes. A linear arrangement based solely on the number of the digits would be unnatural, as I have attempted to show in a recent paper\*. The shape of the snout, whether conical or wedge-shaped, is of importance in tracing lines of descent; this character being also taken into consideration, the species here described as new cannot be placed in the group *Ch. sphenopsiformis*, *delislui*, and *sepioides*, its position being intermediate between *Ch. mionecton* (with four fingers and toes, and 24 or 26 scales round the body), and *Ch. mauritanicus* (with two fingers and three toes, and 10 scales round the body).

\* P. Z. S. 1920, vol. i. p. 77.



41. On the Parasitic Nematoda collected from Mammalian Hosts which died in the Gardens of the Zoological Society of London during the years 1919-1921; with a description of three new Genera and three new Species. By G. M. VEVERS, M.R.C.S., L.R.C.P., F.Z.S., Beit Memorial Research Fellow, and Assistant in the Department of Helminthology, London School of Tropical Medicine.

[Received October 24, 1922: Read November 7, 1922.]

(Text-figures 1-10.)

The parasites referred to in this paper were collected from mammals which died in the Gardens from October 1919 to June 1921, during which period the writer held the position of Honorary Parasitologist to the Society.

In a previous Report, published in 1920 (1), I gave a list of the parasites which were collected during the first eight months of this period. Certain of these are again mentioned in this paper, and to avoid confusion are marked in the Systematic List with an asterisk (\*).

*Leiperenia galebi*, from the Indian Elephant (*Elephas indicus*), and *Galoncus tridentatus*, from the Clouded Leopard (*Felis nebulosa*), have both been described as new species by Dr. M. Khalil in previous papers in 1922 (2). The methods employed in collection have been referred to in my Report of June 1920.

The whole of the material has been worked out in the Helminthological Department of the London School of Tropical Medicine under the Directorship of Prof. R. T. Leiper, to whom I am indebted for his kind assistance and many valuable suggestions.

In all, 43 species were collected from 36 hosts. Three of these are apparently new to science and are described below.

It is necessary to create three new Nematode genera:—

- (1) *Troglostrongylus*, for a new species of Metastrongylid worm found in the frontal sinus of a Leopard Cat (*Felis bengalensis*). Type *T. troglostrongylus*, gen. n., sp. n.
- (2) *Cylicospirura*, for the Spirurid from the stomach of the Tiger originally described as *Spiroptera subequalis* by Molin. Type *C. subequalis* (Molin, 1860), gen. n.
- (3) *Papillosetaria*, for a new species of Filariid worm from the peritoneal cavity of *Tragulus stanleyanus*. Type *P. traguli*, gen. n., sp. n.

In *Tragulus stanleyanus* a second new species also occurred; this I have named *Setaria javensis*, sp. n.

*Systematic List of Nematoda collected.*

*RHABDIASOIDEA* R. & H., 1916.

*ATRACTIDÆ* Travassos, 1919.

\**Leiperenia galebi* Khalil, 1922.

\**Probstmayria vivipara* Ransom, 1907.

*OXYUROIDEA* R. & H., 1916.

*OXYURIDÆ* Cobbold, 1864.

\**Oxyuris equi* Schrank, 1788.

*ASCAROIDEA* R. & H., 1915.

*ASCARIDÆ* Cobbold, 1862.

*ASCARINÆ* Travassos, 1913.

*Ascaris transfuga* Rud., 1819.

*Belascaris marginata* (Rud., 1802), Gedoelst, 1911.

*Belascaris mystax* (Zeder, 1800), Leiper, 1907.

*Toxascaris limbata* R. & H., 1911.

*Toxascaris leonina* (v. Linstow, 1902), R. & H., 1911.

*HETEROCHEILIDÆ* R. & H., 1915.

*GOEZINÆ* Travassos, 1920.

\**Contracacum osculatum* (Rud., 1802), Baylis, 1920.

*HETERAKIDÆ* R. & H., 1914.

*SUBULURINÆ* Travassos, 1914.

*Subulura distans* (Rud., 1809), R. & H., 1912.

*STRONGYLOIDEA* Weinland, 1858.

*STRONGYLIDÆ* Baird, 1853.

*STRONGYLINÆ* Stossich, 1898.

*Strongylus vulgaris* (Looss, 1900), R. & H., 1909.

*Strongylus edentatus* (Looss, 1900), R. & H., 1909.

*Cylicostomum nassatum* (var. *parvum*), Yorke & McFie, [1918.

*Cylicostomum goldi* Boulenger, 1916.

*Cylicostomum bicoronatum* (Looss, 1900), Gedoelst, 1903.

*Esophagostomum apiostomum* (Willach, 1891), R. & H., [1905.

*ANCYLOSTOMINÆ* R. & H., 1909.

[1909.

*Ancylostoma malayanum* (Alessandrini, 1905), R. & H.,

*Ancylostoma ceylanicum* Looss, 1911. [1909.

*Ancylostoma pluridentatum* (Alessandrini, 1905), R. & H.,

*Ancylostoma caninum* (Ercolani, 1859), Hall, 1915.

\**Ancylostoma conepti* Solanet, 1911.

*Galoneus perniciosus* (v. Linstow, 1886), Railliet, 1918.

*Galoneus tridentatus* Khalil, 1922.

\**Uncinaria criniformis* (Goeze, 1782), Railliet, 1899.

*Characostomum asmilium* R. & H. & Joyeux, 1913.



TRICHOSTRONGYLIDÆ Leiper, 1912.

TRICHOSTRONGYLINÆ Leiper, 1908.

\**Hæmonchus contortus* (Rudolphi, 1803), Cobbold, 1898.

METASTRONGYLIDÆ Leiper, 1908.

METASTRONGYLINÆ Leiper, 1908.

\**Troglostrongylus troglostrongylus*, gen. n., sp. n.

SPIRUROIDEA R. & H., 1915.

SPIRURIDÆ Oerley, 1885.

SPIRURINÆ Railliet, 1915.

*Habronema chevreuxi* Seurat, 1913.

*Spirocerca sanguinolenta* (Rud., 1819), R. & H., 1911.

*Streptopharagus armatus* Blanc, 1912.

*Cylicospirura subæqualis* (Molin, 1860), gen. n.

RICTULARIIDÆ Railliet, 1916.

*Rictularia affinis* Jägerskiöld, 1910.

*Rictularia cahirensis* Jägerskiöld, 1910.

*Rictularia plugiostoma* (Wedl, 1861), Will.-Suhm 1873.

GNATHOSTOMIDÆ R. Blanchard, 1895.

*Gnathostoma spinigerum* Owen, 1836.

FILAROIDEA Weinland, 1858.

FILARIIDÆ Claus, 1885.

FILARINÆ Stiles, 1907.

\**Filaria gracilis* Rudolphi, 1809.

*Filaria martis* Gmelin, 1790.

*Setaria labiato-papillosa* (Aless., 1838), R. & H., 1911.

*Setaria hornbyi* Boulenger, 1920.

*Setaria javensis*, sp. n.

*Papillosetaria traguli*, gen. n., sp. n.

TRICHUROIDEA Railliet, 1916.

TRICHURIDÆ Railliet, 1915.

TRICHURINÆ Ransom, 1911.

*Trichuris ovis* (Abildg., 1795), Smith, 1908.

*Trichuris trichiura* (Linnæus, 1771), Stiles, 1901.

ANCYLOSTOMA PLURIDENTATUM (Aless., 1905), R. & H., 1909.

In 1905, Alessandrini described a Hookworm from *Felis mitis*, Brazil, which he named *Uncinaria pluridentatum* (3). In 1909, Railliet and Henry placed the species in the genus *Ancylostoma* (4).

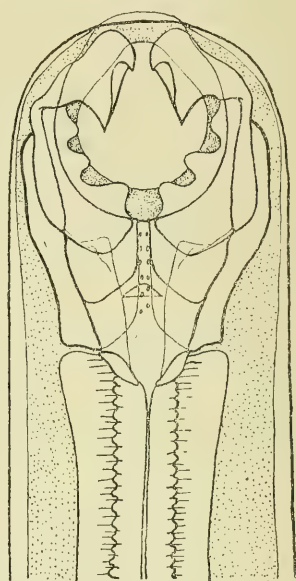
Looss, in his Monograph on the Hookworms (1911) (5), refers

to, and gives a brief description of the worm, with figures copied from the original paper by Alessandrini. The only measurements given are the size of the body. In 1916, Clayton Lane (6) suggested that *A. pluridentatum* might not be a valid species; he also suggested that if Alessandrini had not made an error and the species was valid, it should be made the type of a new genus.

Text-fig. 1.



Text-fig. 2.



*Ancylostoma pluridentatum* (Aless.).

Mouth capsule. Lateral view.

Mouth capsule. Dorsal view.

My material was collected from the small intestine of *Felis tigris*, Malay States.

I have compared the general measurements, mouth capsule, and bursa with the original description and figures given by Alessandrini, and find that they agree in all but three points:—

- (1) The length of the body. Measurements given by Alessandrini: Male 6·8 mm., female 6·5–9 mm.

Measurements of my material from *Felis tigris*:

Male 8·5–9 mm., female 9–10·5 mm.

- (2) The appearance of the mouth capsule when viewed from the dorsal respect. In my specimens the mouth capsule appears much deeper than the mouth capsule in Alessandrini's figure.

- (3) Length of the spicules :

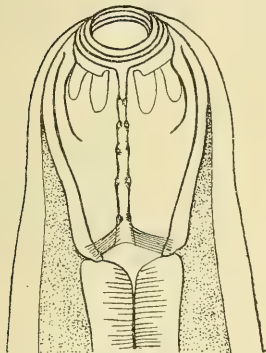
Alessandrini's measurement = 960  $\mu$ .

Material from *Felis tigris* = 800  $\mu$ .

These differences do not seem to indicate that the worms from *F. tigris* are of a different species from those described by Alessandrini from *F. mitis*. The variations noted might well be ascribed to the occurrence in a different host.

It would seem that the figures of the mouth capsule, as given by Alessandrini, were made from somewhat flattened material; I have therefore prepared new figures of the head from the dorsal and lateral aspects (text-figs. 1 & 2).

Text-fig. 3.

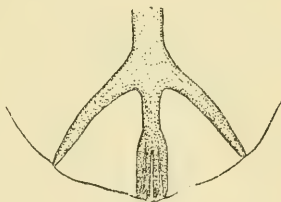


100  $\mu$ .

*Characostomum asmilium* R., H. & Joyeux.

Mouth capsule. Dorsal view.

Text-fig. 4.



Dorsal ray of bursa. ♂.

### CHARACOSTOMUM ASMILIUM R., H. & Joyeux, 1913.

This species was first described by Railliet, Henry and Joyeux in 1913 from *Cercopithecus patas* (7).

These authors describe the worm fully, but do not give figures of the bursa of the male or the cephalic extremity from the dorsal aspect.

Two males were found in the small intestine of a Pig-tailed Macaque (*Macacus nemestrinus*) and one female from a Slow Loris (*Nycticebus tardigradus*).

The opening of the mouth is not terminal, but turns slightly dorsalwards as in *Ancylostoma* and *Necator*.

The buccal aperture is surrounded by three concentric chitinous rings; these have no setæ. The dorsal gutter is very well marked, and is rugose on the dorsal aspect.

A figure is given illustrating these two points, as they are not mentioned in the description of the original material. A diagram of the dorsal ray of the bursa in the male is also given.

#### METASTRONGYLINÆ Leiper, 1908.

##### TROGLOSTRONGYLUS TROGLOSTRONGYLUS, gen. n., sp. n.

In a previous paper (1) I made reference to a parasite which I found in the frontal sinus of a Leopard Cat (*Felis bengalensis*). At that time I was uncertain as to its systematic position, and provisionally diagnosed it as a "species inquirenda" in the genus *Synthetocaulus*, with which it has certain affinities. The female, however, is ovoviviparous, and the male has remarkably long spicules with palmate expansions covered with minute spines, which characters not only establish it as a new species, but separate it from *Synthetocaulus*.

It also has certain characters in common with the genus *Hemostrongylus*, a species of which (*H. subcrenatus*) was described by Railliet and Henry, from the bronchi of a Leopard, in 1913. The disposition of the rays of the bursa in this worm is different; in *H. subcrenatus* the postero-lateral and median-lateral rays are fused, whereas in *T. trogloststrongylus* the antero-lateral and median-lateral rays are joined. *H. subcrenatus*, moreover, has no accessory piece (8).

On these grounds, therefore, I have considered it necessary to create a new genus—*Trogloststrongylus*—for this worm.

It would appear that the only other Nematode parasite which has the frontal sinus as a habitat is the worm *Filaroides mustelarum*, which lives in the frontal sinus of the Weasel (*Mustela vulgaris*) (9).

The systematic position of *F. mustelarum* is somewhat obscure, but it probably falls into the Spiruroidea, which has no affinities with the Strongyloidea, into which *T. trogloststrongylus* belongs. A comparison of these two forms shows certain points of similarity in structure which seem to indicate parallelism in evolution due perhaps to similarity in habitat.

##### TROGLOSTRONGYLUS, gen. n.

*Generic diagnosis.*—*Metastrongylinae*: Head simple, two lips, no buccal capsule. Cuticle covered with fine longitudinal striations. The bursa of the male is small in comparison with the length of the body. The ventral rays are short, and each formed

of two rays fused. The antero-lateral and median-lateral rays are fused together to form one large ray. The postero-lateral and externo-dorsal rays are single and approximately the same size. The dorsal ray is single and broad, owing to the fusion of all its elements.

The spicules are long and equal, they are tessellated throughout and carry pectinate lamellæ along their inner edges; each ends in a palmate expansion, the fingers of which are webbed with a cuticular expansion which bears minute spines. The female is ovoviviparous.

Type-species, *Troglostrongylus troglostrongylus*, sp. n.

TROGLOSTRONGYLUS TROGLOSTRONGYLUS, sp. n.

*Host.* *Felis bengalensis*.

*Locality.* India.

*Habitat.* Frontal sinus.

*Specific diagnosis.*—*Troglostrongylus*: Thin filiform greyish-white worms, tapering rather abruptly at each end.

The mouth is guarded by two inconspicuous lips, each bearing two minute papillæ. There is a slight cuticular expansion at the head and extending about 1 mm. along the body; on this cuticular expansion are faint transverse striations. The rest of the worm is covered with very fine longitudinal striations.

The œsophagus in both sexes is of the simple muscular bulb type, measuring 500  $\mu$  in length and 100  $\mu$  in diameter at the bulb. The excretory pore and nerve ring are situated 250  $\mu$  from the anterior end of the body.

*Male.*—Measures 12 mm. in length by 4 mm. in breadth. The bursa is small and rounded, with a slight median notch in its margin at the point where the distal end of the dorsal ray meets it. The diameter of the bursa is 5 mm. The rays of the bursa are somewhat asymmetrical. The ventral rays are small and double; the antero-lateral and median-lateral rays are fused into one large ray.

The postero-lateral and externo-dorsal rays are single and short, in some cases not reaching the margin of the bursa. The elements of the dorsal ray are fused into one large, broad ray, which terminates in the median notch of the bursa.

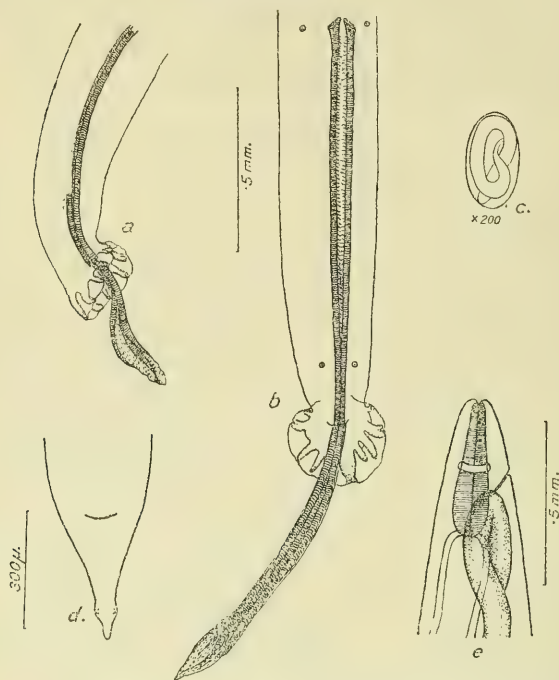
The spicules are equal and measure 2.25 mm. in length; they are dark brown in colour and are tessellated. In addition, along the inner edge of each there are short transverse comb-like projections, which may be single or sometimes divide into two or even three branches. In the distal third these interlock and produce a union of the two spicules. Each spicule ends in a palmate expansion, the cuticular web of which is covered with minute spines. The accessory piece is dagger-shaped and measures 270  $\mu$  in length.



*Female*.—Measures 20–24 mm. in length by .7 mm. in breadth. The tail tapers sharply and ends in a blunt point, near the end of which are situated two small laterally placed papillæ. The anus is  $300\mu$  from the tip of the tail.

The vulva is situated just behind the middle of the body.

Text-figure 5.



*Troglostrongylus troglostrongylus*, gen. n., sp. n.

- a. Caudal extremity of male. Lateral view.
- b. Caudal extremity of male. Ventral view.
- c. Egg.  $\times 200$ .
- d. Caudal extremity of female.
- e. Head of female. Lateral view, showing excretory pore.

The eggs contain a living embryo at birth, and hatching takes place almost immediately, embryos being found in the nasopharynx, lungs, oesophagus, stomach, and intestines. The eggs measure  $87\mu$  by  $70\mu$ . Embryos found in the nasopharynx measured  $240\mu$ .

## SPIRURINÆ Railliet, 1915.

## CYLICOSPIRURA SUBÆQUALIS (Molin, 1860), gen. n.

In 1913, Seurat described a Spirurid from the stomach of *Felis ocreata* Gmelin (10). This worm he considered to be identical with *Spiroptera subæqualis* Molin (11), and placed it in the genus *Spirocerca*, as it conformed in many respects to the type-species of that genus (*Spirocerca sanguinolenta* of the Dog).

He published a description with a drawing of the mouth capsule of the worm taken from a single specimen, which he states was very much flattened by the pressure of the cover-glass. My material consisted of three females and one male collected from the stomach of a Tiger (*Felis tigris*), Malay States.

The measurements of these specimens correspond in every way to those of the worm described by Seurat from *F. ocreata*, except in regard to the mouth capsule, which is much wider in the latter, due no doubt, as Seurat suggests, to the pressure. This writer also states that the chitinous teeth in the mouth capsule are tricuspid, whereas in my specimens they are bicuspid.

Von Drasche in 1882 revised Molin's type material, and figures the cephalic and caudal extremities of the male. In his figure of the mouth-parts he shows each of the chitinous teeth as bicuspid (12).

I have also compared my material with an unpublished drawing of the cephalic extremity made by Prof. R. T. Leiper from Molin's type-specimens in the Vienna Museum, and I find it agrees in every respect.

Seurat, therefore, has either made an error of observation, due perhaps to the flattened state of his specimens, or he has confused another species with *S. subæqualis*, of Molin.

Moreover, as the mouth capsule of this worm with its armature of teeth in no way conforms to the type of the genus *Spirocerca* (*S. sanguinolenta*), I wish to propose a new genus, *Cylicospirura*, with *C. subæqualis* as the type-species.

## CYLICOSPIRURA, gen. n.

*Generic diagnosis.*—*Spirurinae*: Body elongated, tapering slightly anteriorly. Mouth circular, surrounded by six small papillæ. The mouth capsule is deeper and conical in shape, with the apex of the cone in apposition to the anterior end of the œsophagus. It is provided with six triangular chitinous plates arranged radially, each of the internal free ends of which terminates in a bicuspid tooth which projects slightly beyond the entrance to the mouth capsule.

The tail of the male is twisted spirally, and is furnished with a narrow symmetrical bursa, which has four pairs of preanal and two pairs of postanal papillæ. The spicules are unequal, the

long spicule being in the type-species more than five times the length of the short spicule.

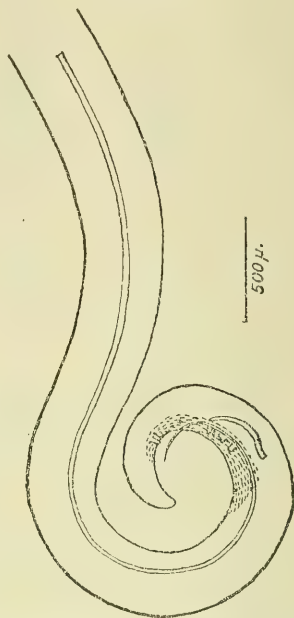
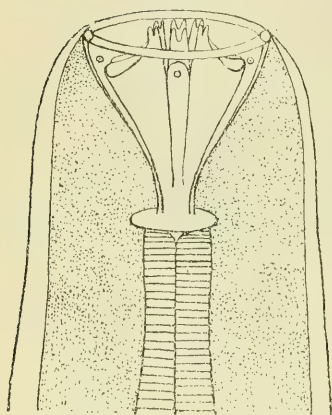
The vulva is situated in the anterior half of the body. The female is ovoviviparous.

Endoparasitic in the stomach of Carnivora.

Type-species, *Cylicospirura subæqualis* (Molin, 1860), gen. n.

Text-fig. 7.

Text-fig. 6.



*Cylicospirura subæqualis* (Molin), gen. n.

Mouth capsule.

Caudal extremity of male.

#### STREPTOPHARAGUS ARMATUS Blanc, 1912.

In 1912, Blanc gave a short description (without figures) (13) of this species in what he termed a preliminary note. As he does not seem to have continued his researches on this worm, I have made some drawings from material collected from a Pig-tailed Macaque (*Macacus nemestrinus*) from India.

No mention is made in the original description of the gubernaculum in the male; this was probably an oversight.

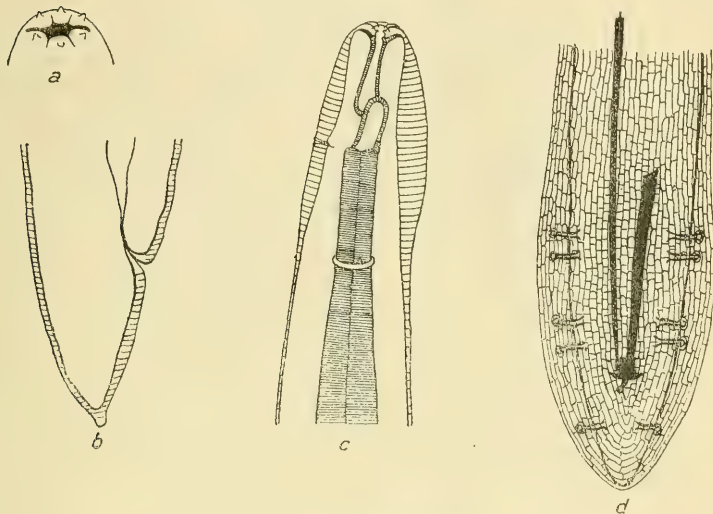
*Spiroptera pigmentata* v. Linstow, 1897 (14), from *Cercopithecus albigularis* Africa, undoubtedly falls into this genus, but must be regarded as a separate species on account of the difference in the length of the spicules.

## SETARIA Viborg, 1795.

From the peritoneal cavity of *Tragulus stanleyanus*, from Java, two species of *Setaria* were recovered: of one species only four females were found, and of the other one male and one female.

Both of these species are apparently new, and one falls into a new genus.

Text-figure 8.

*Streptopharagus armatus* Blanc.

a. Mouth.

b. Caudal extremity of female.

c. Cephalic extremity of male.

d. Caudal extremity of male, showing spicules and accessory piece.

## SETARIA JAVENSIS, sp. n.

*Host.* *Tragulus stanleyanus*.

*Locality.* Java.

*Habitat.* Peritoneal cavity.

*Material.* Four female worms; no males were collected.

*Specific diagnosis.*—*Setaria*: Body tapering gradually towards the anterior end of the body; head rounded and not separated from the rest of the body.

The peribuccal ring is ovoid, the dorso-ventral diameter being greater than the lateral.

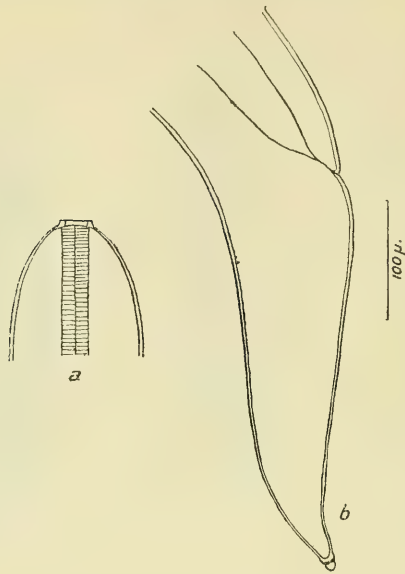
Four submedian head papillæ are present, 40  $\mu$  from the anterior end of the body.

The nerve ring is situated 200  $\mu$  from the opening of the mouth.

*Female* 115 mm. in length and .5 mm. in maximum breadth. Œsophagus has a total length of 7.2 mm. and a maximum breadth of 110  $\mu$ .

The anterior portion of the Œsophagus is 400  $\mu$  in length.

Text-figure 9.



*Setaria javensis*, sp. n.

a. Cephalic extremity of female.

b. Caudal extremity of female.

The anus is distant 320  $\mu$  from the caudal extremity, which tapers gradually and ends in a small knob. The vulva is situated at a point 500  $\mu$  from the anterior end. Ovoviviparous.

The embryos *in utero* measure 210  $\mu \times 7 \mu$ .

In addition to the foregoing species, I recovered another Filariid worm from the abdominal cavity of the same host (*Tragulus stanleyanus*). This species is evidently very closely related to the genus *Setaria*, but there are two points of generic importance which separate it from this genus—namely, the structure of the mouth-parts and the presence of bosses irregularly scattered over the cuticle of both sexes; in other respects it agrees with the generic diagnosis of *Setaria*, as given by Boulenger (15).

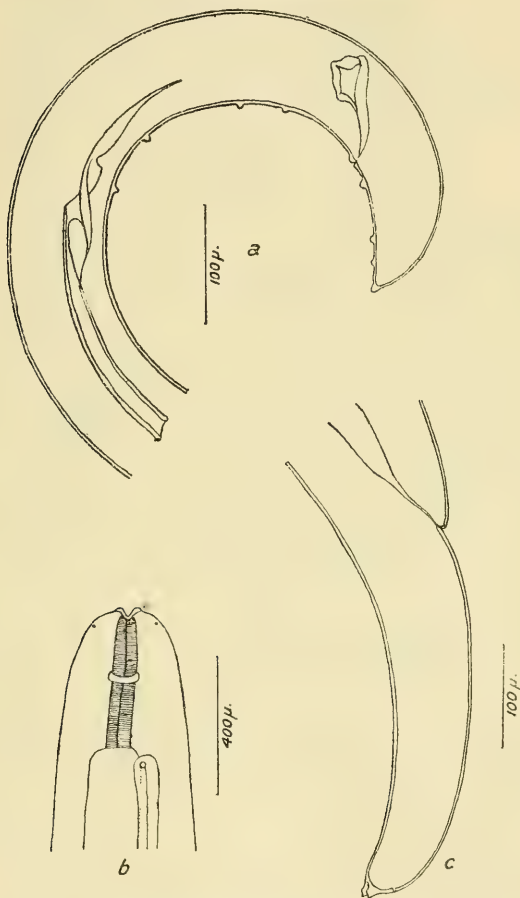


## PAPILLOSETARIA, gen. n.

*Generic diagnosis.*—*Filariinae*: Body cylindrical, filiform, tapering considerably at the posterior extremity in both sexes.

The mouth is guarded by two lateral lips, which are lined by

Text-figure 10.

*Papillosetaria traguli*, gen. n., sp. n.

- a. Caudal end of male, showing spicules and papillæ.
- b. Cephalic extremity of female, showing vulva.
- c. Caudal extremity of female.

an oval ring of chitin. The cuticle of both sexes is covered irregularly with bosses, except in the regions of the head and tail. There are four head papillæ—two lateral and two sub-

median. The œsophagus consists of two parts—a short anterior portion and a longer and thicker posterior portion.

The male is smaller than the female, its attenuated caudal extremity ending in a close spiral. Preanal and postanal papillæ are present. The spicules are unequal, the longer consisting of two parts, the shorter dagger-shaped with an expansion at the proximal end.

The tail of the female is curved dorsally, and bears two lateral appendages close to the caudal extremity. The vulva is near the anterior end of the body. The eggs are thin-shelled. Oviviparous, parasitic in the peritoneal cavity of mammals.

Type-species, *Papillosetaria traguli*, sp. n.

PAPILLOSETARIA TRAGULI, sp. n.

*Host.* *Tragulus stanleyanus*.

*Habitat.* Peritoneal cavity.

*Locality.* Java.

*Specific diagnosis.*—*Papillosetaria*: Body tapering at both extremities, more especially towards the tail. Head rounded, not separated from the remainder of the body. The mouth is guarded by two lips, lined by an oval ring of chitin which projects very slightly beyond the mouth. The head is surrounded by four papillæ: two lateral and two submedian. The body, with the exception of the two extremities, is irregularly studded with small cuticular bosses.

*Male.*—Length 5·7 cm.; maximum breadth 280  $\mu$ .

The anterior portion of the œsophagus measured 500  $\mu$  in length, the posterior region 9·1 mm.

The nerve ring is 200  $\mu$  distant from the anterior end.

The tail is coiled in a close spiral.

The ano-genital opening is 120  $\mu$  from the caudal extremity, which ends in a small rounded knob.

There are three pairs of postanal and four pairs of preanal papillæ.

The spicules are unequal, the larger measuring 370  $\mu$  in length and consisting of two portions—an anterior cylindrical portion and a terminal twisted portion ending in a sharp point.

The shorter spicule is 85  $\mu$  in length, and also consists of two portions—a proximal expanded portion and a distal dagger-shaped portion.

*Female.*—Length 14·5 cm.; maximum breadth 460  $\mu$ .

Anterior portion of the œsophagus is 400  $\mu$  long, the posterior portion 9·6 mm.

The anus is 5 mm. from the caudal extremity; the tail portion has a distinct curve dorsally.

The tail ends in a bifid appendage; near the extremity are two lateral appendages.

The vulva is 650  $\mu$  from the head end.

Oviviparous; embryos measure 230  $\mu$  in length.

## NEMATODE PARASITES ARRANGED ACCORDING TO HOSTS.

## PRIMATES.

## MAMMALIA.

## CERCOPITHECIDÆ.

MACACUS NEMESTRINUS. Pig-tailed Macaque. India.

†*Characostomum asmilium* R., H. & Joyeux, 1913.

*Esophagostomum apiostomum* (Willach, 1891), R. & H., 1905.

*Trichuris trichiura* (Linnæus, 1771), Stiles, 1901.

†*Streptopharagus armatus* Blanc, 1912.

MACACUS RHESUS. Rhesus Monkey. India.

*Esophagostomum apiostomum* (Willach, 1891), R. & H., 1905.

*Trichuris trichiura* (Linnæus, 1771), Stiles, 1901.

†*Spirocerca sanguinolenta* (Rud., 1819), R. & H., 1911.

PAPIO SPHINX. Guinea Baboon. Africa.

*Trichuris trichiura* (Linnæus, 1771), Stiles, 1901.

## CEBIDÆ.

CEBUS FATUELLUS. Brown Capuchin. Guiana.

*Filaria gracilis* Rudolphi, 1809.

LAGOTHRIX INFUMATUS. Smoky Woolly Monkey. S. America.

*Filaria gracilis* Rudolphi, 1809.

CALLITHRIX JACCHUS. Common Marmoset. Brazil.

*Subulura distans* (Rudolphi, 1809), R. & H., 1912.

## PROSIMIÆ.

## LEMURIDÆ.

NYCTICEBUS TARDIGRADUS. Slow Loris. Malay.

†*Ancylostoma malayanum* (Alessandrini, 1905), R. & H., 1909.

†*Characostoma asmilium*, R., H. & Joyeux, 1913.

## CARNIVORA.

## FELIDÆ.

FELIS LEO. Lion. Africa.

*Toxascaris leonina* (v. Linstow, 1902), R. & H., 1911.

FELIS TIGRIS. Tiger. Malay.

*Belascaris mystax* (Zeder, 1800), Leiper, 1907.

*Galonus perniciosus* (v. Linstow, 1886); Railliet, 1918.

*Ancylostoma ceylanicum* Looss, 1911.

†*Ancylostoma pluridentatum* (Alessandrini, 1905), R. & H., 1909.

*Cylicospirura subæqualis* (Molin, 1860), gen. n.

**FELIS PARDUS.** Leopard. India.*Belascaris mystax* (Zeder, 1800), Leiper, 1907.*Gnathostoma spinigerum* Owen, 1836.*Ancylostoma ceylanicum* Looss, 1911.**FELIS NEBULOSA.** Clouded Tiger. Assam.*Belascaris mystax* (Zeder, 1800), Leiper, 1907.*Gnathostoma spinigerum* Owen, 1836.*Galoncus tridentatus* Khalil, 1922.*Ancylostoma ceylanicum* Looss, 1911.†*Habronema chevreuxi* Seurat, 1913.**FELIS VIVERRINA.** Viverrine Cat. India.*Belascaris mystax* (Zeder, 1800), Leiper, 1907.*Ancylostoma ceylanicum* Looss, 1911.**FELIS BENGALENSIS.** Leopard Cat. E. Indies.*Belascaris mystax* (Zeder, 1800), Leiper, 1907.*Gnathostoma spinigerum* Owen, 1836.†*Troglostrongylus troglostrongylus*, gen. n., sp. n.**FELIS SYLVESTRIS.** Wild Cat. Inverness-shire.*Belascaris mystax* (Zeder, 1800), Leiper, 1907.**CYNÆLURUS JUBATUS.** Cheetah. Africa.*Belascaris mystax* (Zeder, 1800), Leiper, 1907.**VIVERRIDÆ.****PARADOXURUS HERMAPHRODITUS.** Malayan Paradoxure.  
Malay.*Gnathostoma spinigerum* Owen, 1836.*Rictularia plagiostoma* (Wedl, 1861), Will.-Suhm, 1873.**MUNGOS MUNGO.** Indian Mongoose. India.†*Filaria martis* Gmelin, 1790.**CANIDÆ.****VULPES VULPES.** Common Fox. Britain.*Belascaris marginata* (Rud., 1802), Gedoelst, 1911.*Rictularia affinis* Jägerskiöld, 1910.*Uncinaria criniformis* (Goeze, 1782), Railliet, 1899.**CANIS LAGOPUS.** Arctic Fox. Arctic regions.*Toxascaris limbata* R. & H., 1911.**CANIS PRIMEVUS.** Indian Hunting Dog. India.*Spirocerca sanguinolenta* (Rud., 1819), R. & H., 1911.**CANIS AUREUS.** Common Jackal. India.*Toxascaris limbata* R. & H., 1911.*Ancylostoma caninum* (Ercolani, 1859), Hall, 1913.

CANIS JUBATUS. Red Wolf. S. America.

*Ancylostoma caninum* (Ercolani, 1859), Hall, 1913.

CANIS OCCIDENTALIS. Arctic Wolf. S. America.

*Toxascaris limbata* R. & H., 1911.

†CANIS AZARÆ. Azara's Fox. S. America.

*Rictularia cahirensis* Jägerskiöld, 1910.

LYCAON CAPENSIS. Cape Hunting Dog. S. Africa.

*Belascaris marginata* (Rud., 1802), Geddoelst, 1911.

*Toxascaris limbata* R. & H., 1911.

#### MUSTELIDÆ.

CONEPATUS PROTEUS. Cordova Skunk. Argentine.

*Ancylostoma conepti* Solanet, 1911.

#### URSIDÆ.

URSUS ARCTOS. Brown Bear. Caucasus.

*Ascaris transfuga* Rudolphi, 1819.

#### OTARIIDÆ.

OTARIA CALIFORNIANA. Californian Sea-Lion. N. Pacific.

*Contracæcum osculatum* (Rud., 1802), Baylis, 1920.

#### PROBOSCIDEA.

##### ELEPHANTIDÆ.

ELEPHAS INDICUS. Indian Elephant. India.

†*Leiperenia galebi* Khalil, 1922.

#### UNGULATA.

##### EQUIDÆ.

EQUUS ONAGER. Onager. African origin. Bred in Gardens.

*Strongylus vulgaris* (Looss, 1900), R. & H., 1909.

*Strongylus edentatus* (Looss, 1900), R. & H., 1909.

*Cylicostomum nassatum* (var. *parvum*), Yorke & McFie, 1918.

*Cylicostomum bicoronatum* (Looss, 1900), Geddoelst, 1903.

*Cylicostomum goldi* Boulenger, 1916.

*Oxyuris equi* Schrank, 1788.

EQUUS GREVYI. Grevy's Zebra. Africa.

*Probstmayria vivipara* Ransom, 1907.

*Cylicostomum nassatum* (var. *parvum*), Yorke & McFie, 1918.

*Strongylus vulgaris* (Looss, 1900), R. & H., 1909.



## BOVIDÆ.

CEPHALOPHUS sp. Duiker. S. Africa.

*Setaria labiato-papillosa* (Alessandrini, 1838), R. & H., 1911.

HIPPOTRAGUS EQUINUS. Roan Antelope. Africa.

†*Setaria hornbyi* Boulenger, 1920.

*Hæmonchus contortus* (Rud., 1803), Cobbold, 1898.

OVIS VIGNEL. Urial Gad. India.

*Trichuris ovis* (Abildg., 1795), Smith, 1908.

AMMOTRAGUS LERVIA. Barbary Sheep. Morocco.

*Hæmonchus contortus* (Rud., 1803), Cobbold, 1898.

## TRAGULIDÆ.

TRAGULUS STANLEYANUS. Stanley's Chevrotain. Java.

†*Setaria javensis*, sp. n.

†*Papillosetaria traguli*, gen. n., sp. n.

[† Signifies that the parasite has not been found in this host before.]

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42. On the Cestode Parasites from Mammalian Hosts which died in the Gardens of the Zoological Society of London during the years 1919-1921; with a description of a new Species of *Cyclorchida*. By G. M. VEVERS, M.R.C.S., L.R.C.P., F.Z.S., Beit Memorial Research Fellow, and Assistant in the Department of Helminthology, London School of Tropical Medicine.

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(Text-figures 11-12.)

During the period under review eleven species of Cestoda were collected from thirteen mammalian hosts dying in the Gardens. One of these is new to science, and has been placed in the genus *Cyclorchida* Fuhr. This is the first record of a member of this genus occurring in a mammal, the only other species (*C. omalancistrotota*) being from a bird (*Platalea leucorodea*). Two of the species are larval forms; of these it is interesting to note *Multiceps* (*Cœnurus*) *serialis* from the lung of the Coypu (*Myopotamus coypus*), bred in Britain. The only other record of the occurrence of this parasite in this particular host is that made by Pagenstecher in 1877, the Coypu in this case being one which had been in captivity in the Berlin Zoological Gardens (1). Apart from this, the only other larval form noted was that of *Tœnia hydatigena* (*Cysticercus tenuicollis*) from three Ungulates.

### *Systematic List of Species.*

#### CYCLOPHYLLIDEA (Adult forms).

MESOCESTOIDIDÆ Fuhrmann, 1907.

MESOCESTOIDES Railliet, 1893.

*M. lineatus* (Goeze, 1782), Railliet, 1893.

ANOPLOCEPHALIDÆ Kholodk, 1902.

ANOPLOCEPHALINÆ R. Blanchard, 1911.

MONIEZIA R. Blanchard, 1911.

*M. expansa* (Rudolphi, 1810), R. Blanchard, 1891.

LINSTOWINÆ Fuhrmann, 1907.

INERMICAPSIFER Janicki, 1910.

*I. pagenstecheri* Janicki, 1910.

*I. settii* Janicki, 1910.

*I. interpositus* Janicki, 1910.

HYMENOLEPIDIDÆ R. & H., 1909.

DIPYLIDIINÆ Stiles, 1896.

CYCLORCHIDA Fuhrmann, 1907.

*C. crassivesicula*, sp. n.

TÆNIIDÆ Ludwig, 1886.

TÆNIINÆ Stiles, 1896.

ECHINOCOCCUS Rudolphi, 1801.

*E. granulatus* (Batsch, 1786), Rud., 1805.

TÆNIA Linnæus, 1758.

*T. tæniæformis* (Batsch, 1786), Wolfhügel, 1911.

*T. balaniceps* Hall, 1910.

CYCLOPHYLLIDÆA (Larval forms).

TÆNIIDÆ Ludwig, 1886.

MULTICEPS Goeze, 1782.

*M. (Cœnurus) serialis* (Gervais, 1847), Stiles & Stev., 1905.

TÆNIA Linnæus, 1788.

*T. hydatigena* Pallas, 1766.

(Syn. *Cysticercus tenuicollis* Rud., 1810.)

#### CYCLOPHYLLIDEA.

MESOCESTOIDIDÆ Fuhrmann, 1907.

*Mesocestoides lineatus* (Goeze, 1782), Railliet, 1893.

The occurrence of this species in a Fox and two Badgers, all from Britain, is interesting, as it opens up the question of the occurrence of two species, *M. lineatus* and *M. litteratus*, in this country, and also throws some light on the question of the validity of the latter species.

Hall stated in 1919 (2) that he could not express an opinion on the validity of *M. litteratus*, but that he retained the name although he could not see any evidence from material or descriptions for supposing that it was a separate species. In the examination of the material from the three hosts mentioned above, certain variations in the size and shape of the head, neck, segments, and internal anatomy were noticed, all of which might be accounted for by differences in the mode of preservation. In the case of the material from one Badger, the host had been dead some time, and the worms were also dead and well extended in consequence; in the case of the other Badger the worms were collected and killed at once, in consequence of which each strobila was much contracted, causing distortion of the internal organs of each segment.



The material from the Fox was dead when preserved, and therefore well relaxed.

I am of opinion that all three batches of material collected from these three hosts belong to the same species (*H. lineatus*), the differences between them being of a transitional or varietal nature, or due to differences in the methods of preservation.

With regard to the validity of the species *M. litteratus*; considering the extreme variability of *M. lineatus*, coupled with the fact that both have been recorded from the same hosts, there seems to be no reason for keeping *M. litteratus* as a separate species, especially as none of the descriptions given for it, including the original by Batsch (1786) (3), contain any points on which to differentiate it from *M. lineatus*.

#### ANOPLOCEPHALIDÆ Kholodk, 1902.

##### LINSTOWINÆ Fuhrmann, 1907.

##### INERMICAPSIFER Janicki, 1910.

(a) *Inermicapsifer pagenstecheri* Janicki, 1910.

(b) *Inermicapsifer settii* Janicki, 1910.

(c) *Inermicapsifer interpositus* Janicki, 1910.

In listing these three species of *Inermicapsifer* from the Rock Rabbit (*Procavia capensis*) I act with great diffidence, my reasons being similar to those given by Douthitt in his monograph on the Anoplocephalidæ, 1915 (4).

It was only by the application of the key to the subfamily Linstowinæ, given by Douthitt, that I was able to make any attempt to diagnose my material.

#### HYMENOLEPIDIDÆ Railliet & Henry, 1909.

##### DIPYLIDIINÆ Stiles, 1896.

##### CYCLORCHIDA Fuhrmann, 1907, e.p. emend.

*Generic diagnosis.* Dipylidiinæ. Rostellum armed with a double crown of hooks which have a very large dorsal root and a small hook portion.

Genital pores unilateral. Genital canals pass between the longitudinal excretory vessels. Cirrus pouch communicating with the genital cloaca by a narrow canal opening upon a large papilla. Testicles very numerous, entirely surrounding the female genital glands. Uterus ventral, growing laterally between the excretory vessels into the cortical parenchyma.

Adults in birds and mammals.

Type-species, *Cyclorchida omalancistrota* (Wedl, 1856), Fuhr., 1907.

*CYCLORCHIDA CRASSIVESICULA*, sp. n. (Text-figs. 11, 12.)

*Host.* *Paradoxurus hermaphroditus* (Pallas).

*Locality.* Malay States.

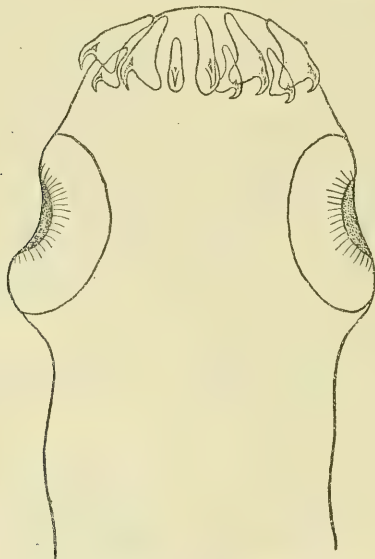
*Habitat.* Small intestine.

Length of strobila 16–20 cm. Maximum width 1–75 mm.

The head is  $250\ \mu$  long by  $280\ \mu$  broad. There are four suckers, each measuring  $100\ \mu$  in diameter. In front of the suckers there is a rostellum  $100\ \mu$  in length and  $200\ \mu$  broad at the base. The rostellum is armed with a double crown of ten large and ten small hooks which interdigitate one with the other.

The large hooks measure  $65\ \mu$  in length from the point of the

Text-figure 11.



*Cyclorchida crassivesicula*, sp. n. Scolex.

hook to the end of the haft, and  $27\ \mu$  from the point of the hook to the end of the guard.

The small hooks measure  $43\ \mu$  from the front of the hook to the end of the haft, and  $13\ \mu$  from the point of the hook to the end of the guard.

The hook portion is relatively very small compared with the basal portion formed by the haft and guard. The neck is  $500\ \mu$  long by  $180\ \mu$  broad. The first segments are equal in width to the neck, and are very short, gradually increasing in both dimensions to the posterior end of the strobila, where they measure  $\cdot 5$  mm. in length by  $1\cdot 75$  mm. in breadth.

In shape the segments are trapezoidal, broader than long, the

posterior border of each segment overlapping the anterior border of the following segment.

The genital pores are unilateral and protrude somewhat.

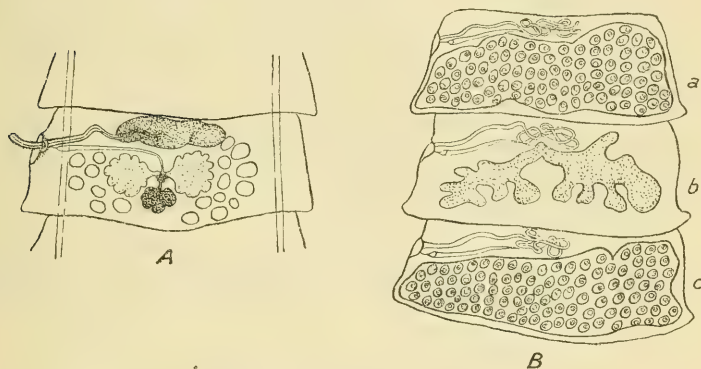
*Male reproductive organs.*

The testes are 16–20 in number, oval in shape, measuring 70–100  $\mu$  in their longest diameter.

In the younger segments they are arranged in a circle round the female genitalia. In the more mature segments they are pushed out laterally by the ovaries but still retain a suggestion of their circular arrangement. There is a large seminal vesicle which lies in the anterior third of the mature segments. In the ripe segments in which the male elements are spent, this vesicle resolves itself into a finely-coiled tube, which is continuous with the vas deferens.

The cirrus pouch is 150  $\mu$  long, and opens through a papilla into the genital atrium or cloaca.

Text-figure 12.



*Cyclorchida crassivesicula*, sp. n.

A. Mature segment, showing male and female genitalia.

B. a and c. Ripe fertile segments.

b. Unfertile segment showing shape of uterus.

In the mature segments the cirrus is extended; it measures 140  $\mu$  in length and 20  $\mu$  in breadth at the base, and is covered with small spines, which are directed backwards.

*Female reproductive organs.*

The two ovaries lie side by side in the centre of the segment; they are round lobulated organs measuring 160  $\mu$ –180  $\mu$  in diameter.

Between the ovaries a very minute shell-gland is situated. Immediately beneath the shell-gland lies a group of yolk-glands, which together form a lobulated kidney-shaped organ measuring

100  $\mu$  in length, having the hilum directed towards the shell-gland. The vagina, which arises from a point between the ovaries, is 165  $\mu$  in length.

As it approaches the genital opening it increases in width to a maximum of 20  $\mu$ , and at a point 30  $\mu$  from the genital aperture it narrows again to a fine duct, and opens into the genital atrium alongside the opening of the cirrus pouch.

The uterus lies horizontally in the segment, and in the unfertilised segment is a sac-like lobulated organ (text-fig. 12, b). In the ripe segment the uterus distends the whole segment and pushes its way to the extreme edges on both sides. The eggs are single, oval in shape, and double-shelled.

The diameters of the outer shell are 140  $\mu \times 100 \mu$ : the embryophore is much smaller, measuring only 40  $\mu$  in diameter. No embryonal hooklets were seen.

In 1908 Smith, Fox, and White (5) described a cestode from *Paradoxurus grayi* which they named *Tenia paradoxuri*. From their description *T. paradoxuri* would seem to have no affinities with *C. crassivesicula*, the rostellum in the former species being unarmed and the genital pores irregularly alternating.

Up to the present the genus *Cyclorchida* is represented by the single species *C. omalancistrota* from the Spoonbill (*Platalea leucorodia*).

*Cyclorchida crassivesicula*, sp. n., agrees with the generic diagnosis of *Cyclorchida* as given by Ransom (1909) (6) in every respect except in the statement that the adults occur only in birds; I have therefore emended the generic diagnosis to read "*Adults in birds and mammals.*"

A comparison of the description of *C. omalancistrota*, as given by Lühe in 1909 (7), with my material offers no point of generic significance upon which to base a different genus.

#### TENIIDÆ Ludwig, 1886.

##### TENINÆ Stiles, 1896.

*Echinococcus granulosus* (Batsch, 1786), Rudolphi, 1805.

The diagnosis of this species, as given by Hall in 1919 (2), is of such latitude as to admit forms showing a variation of almost 100 per cent., and is evidently a careful compilation of the characters as described by various writers. Although there are many cases on record of larval forms which vary considerably from the typical Hydatid produced by the species *E. granulosus*, up to the present the occurrence of more than one species of adult does not seem to have been fully investigated.

Stiles in 1906 (8) suggested that an adult form from the Dingo might be a new species.

Lühe in 1910 (9) redescribed *Tenia oligarthra* Diesing from *Felis concolor*, Brazil, and compared it with *Tenia echinococcus* V. Sieb. From his description it would appear to be a different

species, and therefore should be included in the genus *Echinococcus*. The specimens of adult *Echinococcus* collected from the small intestine of the Cape Hunting Dog (*Lycaon capensis*) agree with the broad diagnosis as given by Hall except in regard to the eggs and the hooks. The eggs in my material measure  $50\ \mu \times 40\ \mu$ , whereas Hall gives  $36\ \mu \times 30\ \mu$  as the maximum. The shape of the hooks in my material differs considerably from the figures of Leuckart and Stiles, the notch between the handle and the guard being exceedingly deep.

I have diagnosed my specimens as *Echinococcus granulosus*, but I do so provisionally, feeling that further study and comparison with forms from other hosts may prove them to be another species.

Until a careful comparison is made of material from Australia, South America, Africa, and Europe it would be unwise to make any definite decision.

*List of Cestode Species arranged under Hosts.*

CARNIVORA.

VIVERRIDÆ.

VIVERRICULA MALACCENSIS. Indian Civet. India.

*Tenia teniæformis* (Batsch, 1786), Wolfhügel, 1911.

GENETTA GENETTA. Common Genet. Spain.

*Tenia teniæformis* (Batsch, 1786), Wolfhügel, 1911.

PARADOXURUS HERMAPHRODITUS. Malayan Paradoxure. Malay.

*Cyclorchida crassivesicula*, sp. n.

CANIDÆ.

VULPES VULPES. Common Fox. Britain.

*Mesocetoides lineatus* (Goeze, 1782), Railliet, 1893.

CANIS AUREUS. Common Jackal. India.

*Tenia balaniceps* Hall, 1910.

LYCAON CAPENSIS. Cape Hunting Dog. S. Africa.

*Echinococcus granulosus* (Batsch, 1786), Rudolphi, 1805.

MUSTELIDÆ.

MELES MELES. Common Badger. Britain.

*Mesocetoides lineatus* (Goeze, 1782), Railliet, 1893.

RODENTIA.

OCTODONTIDÆ.

MYOPOTAMUS COYPU. Coypu. S. America.

*Multiceps (Cœnurus) serialis* (Gervais, 1847), Stiles & Stev., 1905.



## HYRACES.

## PROCAVIIDÆ.

PROCAVIA CAPENSIS. Cape Hyrax. S. Africa.

*Inermicapsifer pagenstecheri* Janicki, 1910.

*Inermicapsifer settii* Janicki, 1910.

*Inermicapsifer interpositus* Janicki, 1910.

## UNGULATA.

## BOVIDÆ.

HIPPOTRAGUS EQUINUS. Roan Antelope. Africa.

*Cysticercus tenuicollis* Rudolphi, 1810.

*Moniezia expansa* (Rud., 1810), R. Blanchard, 1891.

AMMOTRAGUS LERVIA. Barbary Sheep. Morocco.

*Cysticercus tenuicollis* Rud., 1810.

OVIS VIGNEL. Urial Gad. India.

*Cysticercus tenuicollis* Rud., 1810.

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# 43. On a further Collection of Mammals from the Inner Hebrides. By IVOR G. S. MONTAGU, F.Z.S.

[Received October 14, 1922 : Read November 21, 1922.]

(Text-figure 1.)

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(Measurements in the Tables are in millimetres throughout.)

The recent description of Hebridean mammals by G. E. H. Barrett-Hamilton and M. A. C. Hinton in P.Z.S. 1913\* (1), in 'A History of British Mammals' (2), and in Ann. & Mag. Nat. Hist. 1913 (3), and by M. A. C. Hinton in Ann. & Mag. Nat. Hist. 1914 (4), neither completely exhausted the subject nor, in most groups, sought to make any definitive summary. Of the three wild genera most abundantly distributed in the Hebrides—*Sorex*, *Apodemus*, and *Microtus*,—only *Apodemus* has been the subject of a detailed review, which, owing to paucity of material, was of necessity left indeterminate as far as certain islands were concerned. Valuable results were accordingly to be expected from the examination of further mammal material from these localities, and for this reason it was thought desirable to extend the scope, originally of an entomological character, of a private expedition to the Inner Hebrides undertaken by some students at Cambridge University, to include the collection of mammals; specimens, described in this paper, were thus obtained on Islay and Jura by I. G. S. Montagu, and on Gigha by G. E. Hutchinson and G. L. R. Hancock. The results achieved by the inspection of this and other material in the British Museum collection have cleared up several of the indeterminate points in (4), have shown the existence of certain forms of *Sorex araneus* which have an interesting bearing on the history of the species, and have pointed the way to a thorough revision of the British forms of *Microtus*. It should be noted that, again, in the case of no group is a definitive summary attempted; a final view of the relationships of such a group as that treated in this paper is, in the writer's opinion, only possible when forms from all the islands inhabited by that group have been examined. Accordingly the

\* (1) "On a Collection of Mammals from the Inner Hebrides," P. Z. S. 1913.

(2) 'A History of British Mammals,' Gurney & Jackson, 1912-19.

(3) "Three new Voles from the Inner Hebrides, Scotland," A. M. N. H. 1913.

(4) "Notes on British forms of *Apodemus*," A. M. N. H. 1914.

plan here adopted has been the tentative indication of these relationships without final systematic grouping.

It should be noted here that the work of collection in the Inner Hebrides was greatly facilitated by the invariable courtesy of the inhabitants.

The writer further takes this opportunity to express his thanks to M. A. C. Hinton, without whose generous advice the results here described would largely have lacked their comparative value.

*Review of Sorex araneus forms from the Inner Hebrides.*

The satisfactory description of the characters of the Hebridean Common Shrews involves a general survey of those of Great Britain and of the most nearly related Continental forms.

Form.	Dorsal Colour.	Ventral wash.	Size.	p <sup>2</sup> .
<i>S. a. araneus</i> . Continental .....	Dark.	Pale to dark.	Various.	Present.
<i>S. a. castaneus</i> . British Southern	Light.	Pale to dark.	Large.	Present.
<i>S. a. castaneus</i> . Scottish Highland	Light.	Pale to dark.	Small.	Present.
Jura shrew .....	Dark.	Pale.	Small.	Present.
Gigha shrew .....	Dark.	Pale.	Small*.	Present.
Islay shrew .....	Dark.	Absent.	Large.	Absent.

\* With large cranial characters.

It will be seen from the above table that no character can be cited to distinguish the Jura and Gigha shrews from some specimens of the Continental form. Continental *S. a. araneus* includes forms exhibiting distinct local variation from the typical; a small form ranges from Denmark, through Northern Germany and the Netherlands, into France; the large typical form is found not only in Scandinavia but in Southern and Eastern Germany; shrews from the Harz Mountains and from South-Eastern Norway show a light ventral surface, the former thus resembling the Jura and Gigha forms in both size and colour. It should, moreover, be noted that the typical form of *S. a. castaneus* is to be found only in the southern parts of Great Britain, the shrew of the Scottish Highlands being readily distinguishable from it by its generally smaller size and smaller skull. These forms all deserve systematic separation; subspecific status, however, would undoubtedly obscure their relationships in such a manner as to render their present recognition inadvisable. It follows that the revision and satisfactory arrangement of European shrews, as that of any other thoroughly examined group, is impossible without a quadrinomial nomenclature. In the absence of such a nomenclature the writer is unprepared to make, and would certainly regard as unsatisfactory, an attempt to distinguish systematically the forms of Jura and Gigha from *S. a. araneus*. In a similar manner the maintenance of specific status for the Islay shrew obscures its relationships, and the writer accordingly reduces its status to a subspecific one.

It may be noted as an interesting circumstance that the neighbouring Highland form of *S. a. castaneus* is approached in size most closely by the shrew of the island most recently separated from the mainland, Jura, and least by that of the longest separated, Islay. This coincides with the view that smallness in *S. araneus* is a modern character, developed in Scotland, for example, since the separation of Islay from the mainland. Similarly, light dorsal coloration might be regarded as yet more modern, developed throughout Great Britain since the separation of Jura. That largeness in the group is primitive is confirmed by fossil evidence, which can, however, obviously throw no light on the question of ancestral colour. The view that dorsal lightness is primitive in Common Shrews has been considered to be supported by its universal presence in young specimens. If, however, this latter view be correct, the Jura and Gigha shrews must have an unusual history; on the one hand they may be regarded as convergent forms, strikingly parallel with Continental *S. a. araneus*; on the other hand they must be regarded as representatives of a successful modern group, which, having excluded the older light group from the European mainland, has itself, in part, been excluded from the British mainland. The improbability of both these assumptions encourages the statement that the description of the Jura and Gigha shrews tends to confirm the view that dorsal lightness in *S. a. castaneus* is a secondary development from a dorsal clove-brown condition; this view is perhaps supported by the fact that, even in *S. a. castaneus*, the young coat is of a slightly lighter tint than is that of the average adult.

#### SOREX ARANEUS ARANEUS Linnæus.

*Sorex araneus castaneus* Barrett-Hamilton & Hinton, P. Z. S. 1913, p. 823 (1).

*Material examined and Dimensions.* Six adults (3 ♂, 3 ♀) collected by Sheppard in May 1912 in Jura. Five adults (2 ♂, 3 ♀) and six young adults (3 ♂, 3 ♀) collected by Hutchinson in June and July 1922 in Gigha.

JURA.		HB.	T.	HF.
Average of six adults .....		72.5	35.3	12
GIGHA.				
2.	Adult ♂, 30.6.22. ....	70	37	13
5.	" ♂, 30.6.22. ....	76	40	14
6.	" ♀, 30.6.22. ....	70	32	11.5
11.	" ♀, 2.7.22. ....	71	34	12.5
15.	" ♀, 3.7.22. ....	77	37.5	12
1.	Young adult ♂, 30.6.22. ....	62	35*	12
10.	" " ♂, 2.7.22. ....	63	37	13
14.	" " ♂, 3.7.22. ....	66.5	34	12
3.	" " ♀, 30.6.22. ....	71	39.5	13
4.	" " ♀, 30.6.22. ....	68.5	38	12
7.	" " ♀, 1.7.22. ....	59	36	12
Average of five adults .....		72.8	38.3	12.6

The term "young adult" is applied to specimens in the light summer coat, their feet being abundantly clothed with hair.

\* Tail damaged in trap.



*Description.* Both these forms exhibit a dark, clove-brown, dorsal coloration and a light ventral surface with traces of pale wash; they are thus indistinguishable in appearance from certain specimens of Continental *S. a. araneus*. In size (head-and-body and condylobasal lengths) they resemble the neighbouring Highland *S. a. castaneus* in being small. The Gigha form, however, has large cranial and jaw measurements not usually associated with small length of skull. This may represent a secondary development, or may represent certain survived characters from the primitive general largeness. The sum of these characters indicate that the Jura and Gigha shrews exhibit considerably more affinity with *S. a. araneus* than with *S. a. castaneus*, and it would certainly be incongruous to leave them with the latter group. While they exhibit sufficiently distinct combinations of characters to justify separate recognition, the writer does not propose, for reasons stated elsewhere, to obscure their relationships by systematising them as subspecies.

*SOREX ARANEUS GRANTII* Barrett-Hamilton & Hinton.

*Sorex grantii* Barrett-Hamilton & Hinton, P. Z. S. 1913, p. 824 (1).

*Habitat.* Islay.

*New Material examined and Dimensions.* Five adults (2 ♂, 3 ♀), one young adult (♀), and one aged specimen (♂) collected by Montagu in June 1922.

	HB.	T.	HF.
8. Adult ♂, 18.6.22. ....	74	37	12
11. „ ♂, 18.6.22. ....	66	35	12
3. „ ♀, 17.6.22. ....	72	31	12
7. „ ♀, 18.6.22. ....	77	37	12
9. „ ♀, 18.6.22. ....	76	38	11.5
15. Young adult ♀, 21.6.22. ....	72	40	12
12. Aged ♂, 19.6.22. ....	60	39	13
Average of 1922 adults (5) ....	73	35.6	11.9
„ of all adults (23) ....	76.15	35.9	12.45

*Description.* The new specimens of this form confirm the description by Barrett-Hamilton and Hinton in (1). An examination of all specimens gives the following figures:—

$p^2$  present on both sides in 10 specimens, 45 p.c. of those examined.

„ „ „ one side „ 5	„ 23	„ „ „
„ „ „ both sides „ 7	„ 32	„ „ „

No. 12 is a most remarkable specimen, the discovery of which has an important bearing on the bionomics of the shrew. L. E. Adams collected data, his interpretation of which has been generally accepted, demonstrating that *S. a. castaneus* is an



annual, each generation surviving about eighteen months. Thus, according to this hypothesis:—

In spring and early summer of year  $x$  there are present adults of year  $x-1$  and young of year  $x$  being produced.

In late summer and autumn of year  $x$  there are present young adults of year  $x$  and adults of year  $x-1$  dying off.

In winter of years  $x$ — $x+1$  there are only adults of year  $x$  generation.

The abundant data in support of this view need not be recapitulated, suffice it to say that all winter specimens were found to be indistinguishable in point of age, and that no really aged specimen had hitherto been examined. This theory was extended to embrace many other European shrew forms. No. 12, however, is undoubtedly above normal age; the teeth are almost completely worn away, the dorsal black and the ventral silver coats are grizzled. No specimen like it is in the British Museum collection, nor has one been recorded. It should be noted that the proportion (1/29th) of examined *S. a. grantii* specimens that this individual represents does not encourage the view that there is a tendency to longevity in the subspecies, but causes one to regard its occurrence as being as exceptional as in *S. a. castaneus*.

In reducing the status of this form to a subspecific one the writer is following the method of Barrett-Hamilton and Hinton, who, on p. 432 of (2), write: "This mouse (*M. a. macgillivrayi*) might well be called a species were it not that the subspecific name indicates its relationships." From this point of view specific status was, in the first place, incongruous for the Islay shrew, and the necessity for systematising it as a subspecies of *S. araneus* has been enhanced by the description of the shrews from Jura and Gigha, the characters of which emphasize the relationships of the Islay form. It should be added that this view is acceptable to M. A. C. Hinton.

#### SOREX MINUTUS MINUTUS Linnæus.

*Material examined and Dimensions.* One adult (♀) collected by Montagu in June 1922 in Jura.

	HB.	T.	HF.
17. Adult ♀, 23.6.22. . . . .	59	38*	11
Average of sixteen adults from the Inner Hebrides (1)	55.5	35.4	10.1

\* Tail damaged in trap.

*Description.* This shrew has now been reported in the Hebrides from Lewis, N. Uist, Benbecula, S. Uist, Barra; Skye, Sanday, Eigg; Coll, Tiree; Islay, Jura, Gigha; Great Cumbrae, Arran, Bute. It had not hitherto been reported from Jura. The present specimen, it should be noted, is noticeably large in all dimensions.

*Sorex* skull dimensions.*Sorex araneus araneus*.

JURA.	Cbl.	Mb.	Bbc.	Dbc.	M.
Average of three specimens .....	18.50 (2)	5.15	9.10 (2)	4.85 (2)	9.34
GIGHA.					
5. Adult ♂ .....	18.39	5.64	9.66	5.23	9.68
15. " ♀ .....	18.62	5.38	6.60	5.35	9.62
7. " Young adult ♂ .....	18.44	5.36	9.50	5.33	9.73
Average of eight specimens .....	18.55 (4)	5.39	9.56 (4)	5.30 (3)	9.74

*Sorex araneus grantii*.

ISLAY.					
8. Adult ♂ .....	18.71	5.30	9.27	5.23	9.65
11. " ♂ .....	18.81	5.42	9.24	5.40	9.57
3. " ♀ .....	19.06	5.65	9.50	5.33	9.82
7. " ♀ .....	19.22	5.38	9.22	5.16	9.70
12. Aged ♂ .....	18.98	5.50	9.77	5.00	9.76
Average of nineteen specimens ...	18.85 (18)	5.32	9.26 (16)	5.15 (18)	9.65

*Sorex minutus minutus*.

JURA.					
17. Adult ♀ .....	15.94	4.33	7.45	4.35	7.89

*Notes on Apodemus.*

Hinton remarks, on p. 119 of (4), that "in practically every island of the Hebrides, differentiation from the parent stock has proceeded so far that the most logical course would be to describe the mice of each island as a distinct subspecies." In his paper, however, lack of abundant material compelled him temporarily to group the mice of Ghia and Tiree with those of Great Cumbrae as *A. h. cumbrae*, and the mice of Jura and Islay with those of Mull as *A. h. macleani*. The distinguishing characters he observed in them are well confirmed by the extended series now available, and others are made apparent; there is left no doubt of the distinct nature of each, which is accordingly here separated.

*APODEMUS HEBRIDENSIS TIRÆ*, subsp. n.

*Apodemus hebridensis cumbrae* Hinton, A. M. N. H. 1914, p. 128 (4).

*Habitat.* Tiree.

*Material examined and Dimensions.* Four adults (3 ♂, 1 ♀) collected by Sheppard in July 1912.

	HB.	T.	HF.	E.
Type 150. Adult ♀, 13.7.12. ....	100	88	22	13.5
Average of all adults (4) .....	102.5	84.25	23.1	13.5

*Description.* In general dorsal colour this form nearly resembles *A. h. cumbrae*; the flanks are slightly less bright than those of *A. h. cumbrae*, and are little lighter than the back. The contrast between flanks and belly is not striking; the latter is silvery, with slight trace of the pectoral spot.

The size of this form is greater than that of the other rufous mice, *A. h. cumbræ* and *A. h. ghia*, with which it was formerly associated. The tails are short, and the ears are considerably shorter than those of other forms of *A. hebridensis*.

The only complete skull available, though that of an old specimen, is noticeably small. The dimensions indicate a broad rostrum like that of the Sodor (Gigha, Jura, Islay) forms, and a peculiar long, narrow nasal; in other proportions the skull seems fairly to resemble that of the Cumbræ form.

*APODEMUS HEBRIDENSIS GHIA*, subsp. n.

*Apodemus hebridensis cumbræ* Hinton, A. M. N. H. 1914, p. 128 (4).

*Habitat.* Gigha.

*Material examined and Dimensions.* One adult (♀) collected by Sheppard in May 1912. Three adults (♂) collected by Hancock and Hutchinson in July 1922.

	HB.	T.	HF.	E.
8. Adult, 1. 7. 22. ....	94	89	23	14.5
<i>Type</i> 4. „ 2. 7. 22. ....	92	95	23	15.5
7. „ 3. 7. 22. ....	97	88*	25	15
Average of all adults .....	95.75	89.7	23.4	15

\* Tail damaged in trap.

*Description.* The black dorsal hairs are distributed, not so as to dull the general colour from rufous to brown as in the Mull, Islay, Jura, and typical *A. h. hebridensis* forms, but in more definite splashes; thus the back remains rufous with black spangled more abundantly in a median position than on the flanks. There is bright contrast between the flanks and the silvery belly, the line of demarcation being distinct. The pectoral spot is slight, though more distinct than in *A. h. cumbræ* and *A. h. tiræ*.

The appendage measurements correspond to those of *A. h. cumbræ* and the typical form.

The skull measurements, when compared with those of *A. h. cumbræ*, indicate a relatively small zygomatic breadth, cranial width, and coronal cheek-teeth length. In these measurements the skull of *A. h. ghia* more closely resembles that of the Islay than that of the Cumbræ form.

*APODEMUS HEBRIDENSIS TURAL*, subsp. n.

*Apodemus hebridensis maclean* Hinton, A. M. N. H. 1914, p. 130 (4).

*Habitat.* Islay.

*Material examined and Dimensions.* Seven adults (2 ♂, 5 ♀) collected by Sheppard in May and August 1912, two adults (?)

in the Royal Scottish Museum, and four adults (3 ♂, 1 ♀) and one young specimen (♂) collected by Montagu in June 1922.

	HB.	T.	HF.	E.
Type 2. Adult ♂, 17. 6. 22. ....	91	91	25	15
4. „ ♂, 18. 6. 22. ....	97	98	26	16
14. „ ♂, 20. 6. 22. ....	98	89	23	14
5. „ ♀, 18. 6. 22. ....	91	88	24	16
1. Immature ♂, 16. 6. 22. ....	62	62	24	14
Average of 1922 adults (4).....	94.25	91.5	24.5	15.25
„ „ all adults (13) .....	93.6	84.6	23.1	14.4

*Description.* This form well resembles *A. h. maclean* in general colour; there is, however, less contrast between the back and flanks, the latter being distinctly more rufous than the lighter flanks of *A. h. maclean*. The ventral surface is silvery and the pectoral spot even less distinct than in *A. h. maclean*.

The appendage measurements of Sheppard have often been found to require revision, and the fact that in this case they do not agree with those of Montagu indicates that too much reliance should not be placed on them. There can, accordingly, be little doubt that the ears of Islay mice are longer than those of the Mull form, with which they were formerly associated. The tail, also, like that of the Cumbrae, Gigha, and Jura mice, is noticeably longer than that of the Mull and typical *A. h. hebridensis* forms. The hind feet, far from being small as suggested on p. 130 of (4), are extremely large; it may be noted that in the young specimen the hind foot is equal to 40 per cent. of the head and body length.

The measurements of the recently collected skulls largely confirm the differences noted by Hinton in comparing this form with *A. h. maclean*. The skull of *A. h. tural* is to be distinguished from the latter by its greater zygomatic and interorbital breadths, broader and deeper brain-case, rather larger bullæ, and broader rostrum and masseteric plate.

#### APODEMUS HEBRIDENSIS LARUS, subsp. n.

*Apodemus hebridensis maclean* Hinton, A. M. N. H. 1914, p. 130 (4).

*Habitat.* Jura.

*Material examined and Dimensions.* Three adults (2 ♂, 1 ♀) collected by Sheppard in May 1912, and two adults (♀) collected by Montagu in June 1922.

	HB.	T.	HF.	E.
Type 123. Adult ♂, 18. 5. 12. ....	100	59*	23	14.5
19. „ ♀, 26. 6. 22. ....	86	75	23	15.5
20. „ ♀, 26. 6. 22. ....	84	94	23	15.5
Average of all adults (5) .....	92.6	83.7	22.8	14.8

\* Tail damaged in trap.

*Description.* This form resembles *A. h. tural* in general colour, but is dorsally darker, being the darkest form of *A. hebridensis*; the dark hairs are distributed evenly, though more abundant in a median position. The ventral surface is silvery and the pectoral spot is faint.

The appendage measurements resemble those of *A. h. tural*, the ears being longer than those of *A. h. maclean*.

Like *A. h. tural* the skull measurements resemble those of *A. h. hebridensis* and differ from those of *A. h. maclean* in showing larger zygomatic, interorbital, and cranial breadths, larger cranial depth, and broader rostrum and masseteric plate. The skull, however, resembles that of *A. h. maclean* and differs from that of *A. h. tural* in the smallness of its bullæ; further, it shows a peculiarly large width of the incisive foramina.

*Apodemus* skull dimensions.

No.	(3) Gt. Cumbræ. <i>A. h.</i> <i>cumbræ.</i>	(2) Tirée. <i>A. h.</i> <i>tiræ.</i>	(2) Gigha. <i>A. h.</i> <i>ghia.</i>	(8) Islay. <i>A. h.</i> <i>tural.</i>	(4) Jura. <i>A. h.</i> <i>larus.</i>	(3) Mull. <i>A. h.</i> <i>maclean.</i>
1.	23·16	22·70	24·36	23·53	23·84	23·73
1 <i>a.</i>	100	100	100	100	100	100
2.	110·75	110·00	107·90	109·36	109·40	109·83
3.	56·56	56·00	53·40	54·20	54·65	53·03
4.	16·80	17·40	17·60	17·69	17·50	17·28
5.	51·00	50·50	48·20	48·66	49·38	48·26
6.	35·60	35·50	35·72	35·13	34·99	34·06
7.	45·56	46·30	46·20	45·78	46·03	45·90
8.	26·60	26·45	26·37	26·39	25·81	25·93
9.	40·23	42·10	39·45	40·05	40·85	41·80
10.	11·91	11·70	11·90	11·97	12·08	11·93
11.	54·33	55·95	55·90	54·34	54·65	54·03
12.	28·90	28·65	29·08	29·34	29·47	29·90
13.	23·56	24·70	22·22	23·40	24·09	24·70
14.	7·46	7·73	8·66	8·13	9·09	6·86
15.	18·96	19·80	19·62	19·30	19·94	18·83
16.	10·66	10·35	11·41	10·77	11·89	10·26
17.	16·25	16·25	16·02	15·92	16·22	16·05

Number in ( ) of skulls on which averages are based.

- |                                                         |                                        |
|---------------------------------------------------------|----------------------------------------|
| 1. Condylbasal length: average in millimetres.          | 8. Condyle to front surface of bulla.  |
| Reductions:—                                            | 9. Nasal length.                       |
| 1 <i>a.</i> Condylbasal length equals 100.              | 10. Nasal width.                       |
| 2. Occipitonasal length.                                | 11. Palatal length.                    |
| 3. Zygomatic breadth.                                   | 12. Diastema.                          |
| 4. Interorbital constriction.                           | 13. Length of incisive foramina.       |
| 5. Cranial width.                                       | 14. Width of incisive foramina.        |
| 6. Cranial depth, in middle.                            | 15. Rostral breadth.                   |
| 7. Postmolar length; condyle to <i>m</i> <sub>3</sub> . | 16. Width of masseteric plate (least). |
|                                                         | 17. Cheek-teeth, coronal length.       |



*MUS MUSCULUS MUSCULUS* Linnæus.

*Material examined and Dimensions.* Three (2 ♂, 1 ♀) collected by Montagu in June 1922 in Islay, and one (♂) collected by Montagu in June 1922 in Jura.

ISLAY.	HB.	T.	HF.	E.
10. Adult ♂, 18. 6. 22. ....	82	82	18	13
13. „ ♂, 20. 6. 22. ....	78	76*	17	13
6. „ ♀, 18. 6. 22. ....	75	75	17	10
JURA.				
18. Adult ♂, 25. 6. 22. ....	71	71	17.5	13

\* Tail damaged in trap.

*Description.* All the specimens, which were trapped in fields, are in the yellowish outdoor pelage.

*Review of the British forms of* *Microtus agrestis*.

Definitions of various subspecies of *M. agrestis* have appeared from time to time (1, 2, 3) describing forms from the Hebrides and from the Scottish mainland. These definitions, however, have been written not by the same person, and often without facilities for surveying the whole material from all these localities; the existing descriptions accordingly lack comparative value in some respects, such as character of fur; for such characters are largely incapable of reference to other than subjective standards. The writer therefore gives here, in tabular form, a comparison of the various types of fur recognised as peculiar in British *M. agrestis* forms.

No.	TYPICAL.	ISLAY.	GIGHA.	Eigg.	MUCK.
1.	Intermediate.	Sleek.	Shaggy.	Shaggy.	Shaggy.
2.	Soft.	Soft.	Harsh.	Soft.	Soft.
3.	Rufous.	Rufous.	Rufous.	Rufous.	Rufous.
4.	12	10	14	14	14
5.	2	2	2	2	2
6.	General.	General.	Abundant.	General.	General.
7.	16	16	16	16	16
8.	Irregular yellow.	Uniform dark grey.	<i>a</i> and <i>b</i> .	Uniform white.	More uniform yellow.
9.	6	6	6	6	6
10.	Grey, 2	Grey, 2	Grey, 2	White, 2	Grey, 2
11.	8		8		8
12.	Pale, 2		Bright, 2		Pale, 2

*a*, irregular yellow; *b*, uniform dark grey.

Dorsal fur characters:—

1. Appearance.
2. Texture.
3. General colour.
4. Coloured hair, length grey bases.
5. „ „ „ coloured tips.
6. Black hair, distribution.
7. „ „ length.

Ventral fur characters:—

8. General colour.
9. Short hairs, length grey bases.
10. " " " and colour tips.
11. Longer hairs, length grey bases.
12. " " " and colour tips.

Muck, *M. a. luch*; Eigg, *M. a. mial*; Gigha, *M. a. fiona*; Islay, *M. a. macgilivraii*; Typical, *M. a. exsul*; N. Uist, S. Uist, Jura, Arran, Mull, *M. a. neglectus*; Mainland, Bute.

An examination of the skulls from all the localities visited leads to the conclusion that the present systematic grouping, based on the degree of reduction of the 4th inner angle of *m1*, is an inaccurate one. This character is one which, seldom constant even locally, varies very readily, and undoubtedly its variation does not correspond with degree of differentiation in other

Text-figure 1.

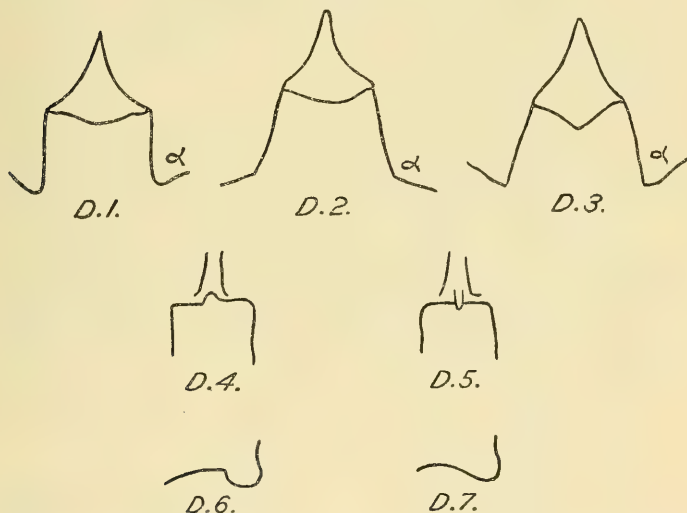


Diagram 1. Temporal shield: Type 1. D.2. Temporal shield: Intermediate type. D.3. Temporal shield: Type 3. D.4. Posterior part of palate: Type 2. D.5. Posterior part of palate: Type 1. D.6. Anterior part of jugal of *M. a. fiona*. D.7. Anterior part of normal jugal.

respects from the primitive type. Steps are being taken to secure specimens from most of the hitherto unvisited islands, and M. A. C. Hinton and I. G. S. Montagu are undertaking a definitive revision of the group. Accordingly, in spite of the incongruous position of many *M. agrestis* forms, no attempt is

made here to define them in conformity with the present estimate of their position. An exception is, however, made in the case of *M. a. fiona* of Gigha since the material representing it is new and undescribed. It is further considered advisable to indicate the lines along which the projected new groupings will be effected.

### Group 1.

Temporal shield type 1.

*M. a. macgillivrayi*. Islay.

Fur colour peculiar; palate type 1; 4th i. a. distinct.

*M. a. exsul*. Jura.

Fur colour typical; palate type 1; 4th i. a. distinct or vestigial.

### Intermediate Group.

Temporal shield intermediate type.

*M. a. fiona*. Gigha.

Fur colour peculiar; palate type 2; 4th i. a. vestigial; jugal peculiar.

### Group 3.

Temporal shield type 3.

Division 1. Palate type 1.

*M. a. mial*. Eigg.

Fur colour peculiar: 4th i. a. distinct.

*M. a. exsul*. N. Uist, S. Uist.

Fur colour typical; 4th i. a. distinct.

*M. a. exsul*. Mull.

Fur colour typical; 4th i. a. distinct or vestigial.

Mixed Division. Palates of both types.

*M. a. neglectus*. Mainland.

Fur colour typical; 4th i. a. distinct, vestigial, or absent.

Division 3. Palate type 2.

*M. a. neglectus*. Bute.

Fur colour typical; 4th i. a. distinct, vestigial, or absent.

*M. a. exsul*. Arran.

Fur colour typical; 4th i. a. distinct or vestigial.

*M. a. luch*. Muck.

Fur colour peculiar; 4th i. a. distinct, vestigial, or absent.

*MICROTUS AGRESTIS FIONA*, subsp. n.

*Microtus agrestis exsul* Barrett-Hamilton & Hinton, P. Z. S. 1913, p. 830 (1).

*Habitat*. Gigha.

*Material examined and Dimensions*. One adult (♂) collected by Sheppard in May 1912, six adults (3 ♂, 3 ♀) and two immature specimens (1 ♂, 1 ♀) collected by Hancock and Hutchinson in June and July 1922.

		HB.	T.	HF.	E.
	3. Adult ♂, 1.7.22. ....	119	39	18	12
Type	5. „ ♂, 2.7.22. ....	121	35	20	11.5
	9. „ ♂, 2.7.22. ....	129	38	19	11.5
	1. „ ♀, 30.6.22. ....	107.	35	19	11
	6. „ ♀, 2.7.22. ....	113	36	18	12.5
	12. „ ♀, 2.7.22. ....	117	34	19	12
	13. Immature ♂, 2.7.12. ....	97	31	19	9
	2. „ ♀, 30.6.22. ....	97	32	18	9.5
	Average of all adults (7) .....	118.7	35.7	18.7	11.8

*Description.* This form is, externally, of peculiar appearance. The long dorsal fur is darkened, and rendered harsh by the profuse abundance in it of long black hairs. There appear to be present in the subspecies two types of ventral surface; this diversity may prove to be a secondary sexual character. Females 1, 12, 2 (imm.) have ventrally only short grey hairs, and exactly resemble in this respect *M. a. macgillivraii*. Males 3, 5, 9, 13 (imm.), 127 and female 6 have, besides the short grey hairs, longer hairs with tips pigmented brighter yellow than those of the typical form, and distributed in similar irregular patches. The character of No. 6 prevents one from formulating a definite opinion of the nature of this diversity until further material is available.

In general body size and dimensions of appendages this form resembles *M. a. exsul*.

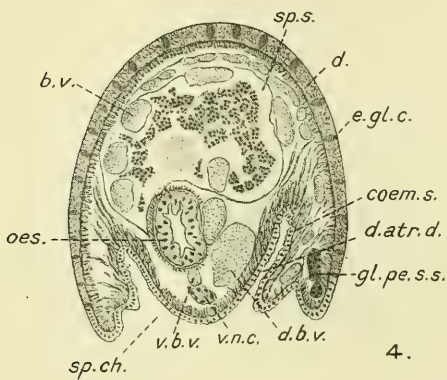
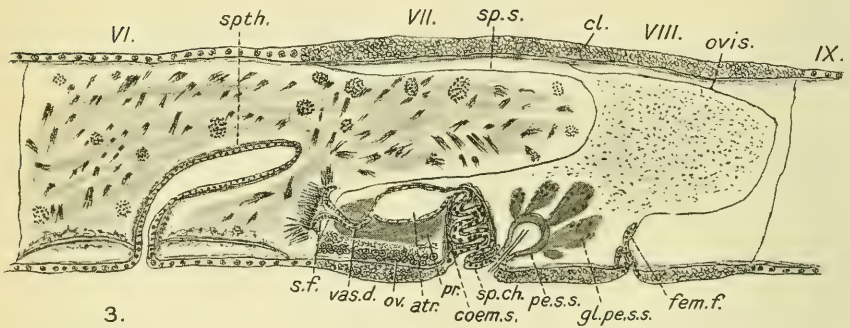
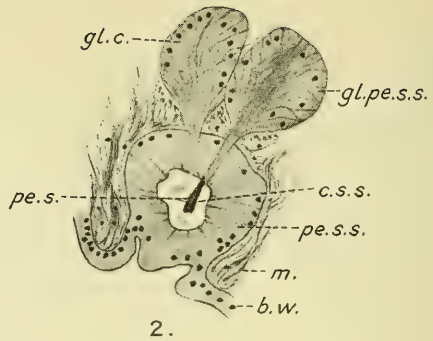
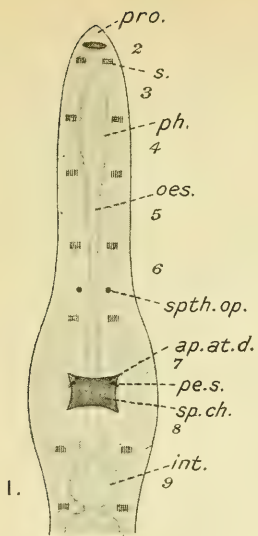
The skull shows a temporal shield like that of *M. a. exsul* in its main characters, but resembling that of *M. a. macgillivraii* in certain minor respects. The shield is, further, unique in showing angle  $\alpha^*$  greater than  $90^\circ$ ; in all other forms examined this angle is less than  $90^\circ$ . The posterior part of the palate is grooved. The jugal is peculiar in showing in dorsal view an abrupt anterior curve about 3 mm. from its junction with the rostrum. The 4th inner angle of  $m_1$  is distinguishable in all specimens but is never more than vestigial.

\* See Diagram 2.

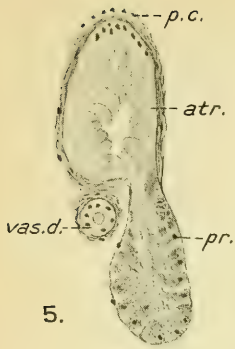




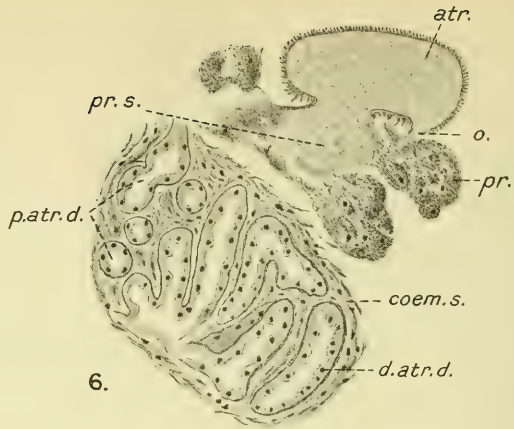




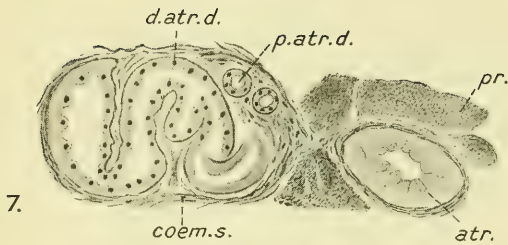




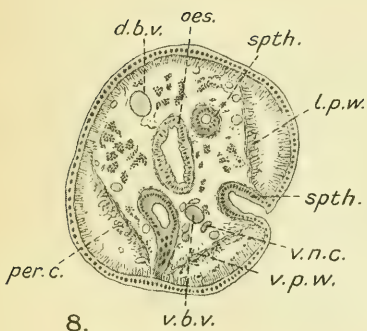
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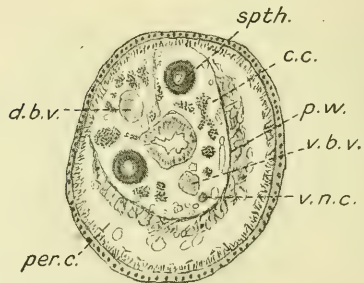
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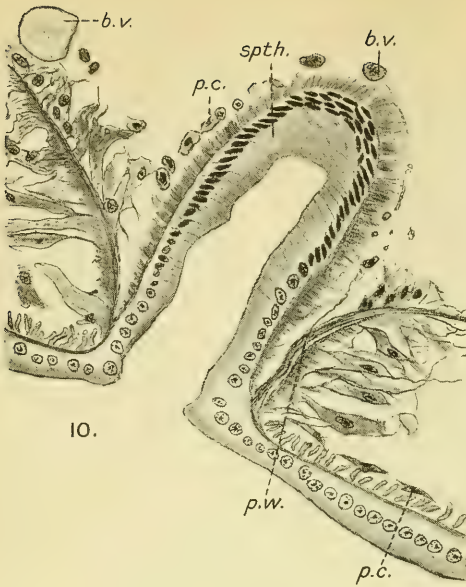
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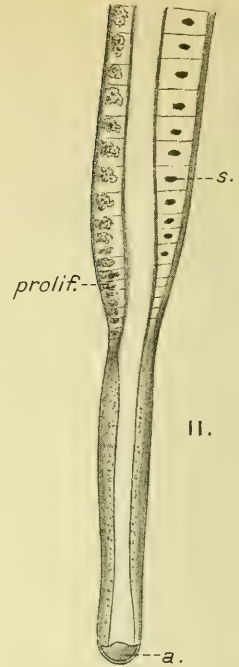
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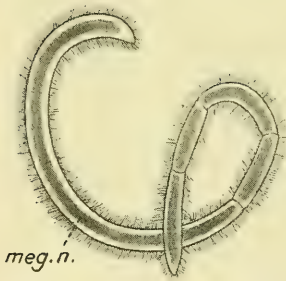




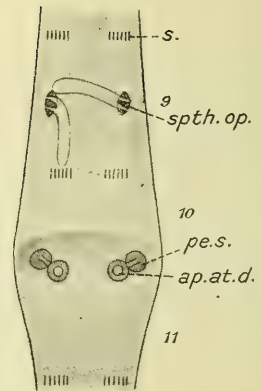
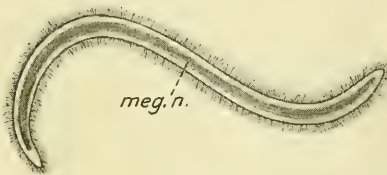
10.



11.



12.



13.

44. Two New Indian Species of the little-known Genus *Aulodrilus* Bretscher of the Aquatic Oligochaeta belonging to the Family Tubificidae. By H. R. MEHRA, M.Sc., Zoological Department, Benares Hindu University. (From the Zoological Laboratory, Cambridge.) \*

[Received July 27, 1922 : Read November 21, 1922.]

(Plates I.-III.†; Text-figures 1-9.)

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## (1) INTRODUCTION AND PREVIOUS WORK ON THE GENUS.

The material which forms the subject of this paper was obtained from the mud at the bottom of a big pond known as Rewari-talab in Benares. This pond has its source of supply in the waste water from the city waterworks, in which the water from the Ganges is mainly used for the supply of the town.

In the same mud were also found many specimens of *Limnodrilus socialis* Stephenson and *Branchiura sowerbyi* Beddard, common Indian Tubificids; *Branchiodrilus hortensis* Stephenson, *Dero limosa* Leidy, and *Aulophorus furcatus* Oken, gilled Naidomorphs. Till recently the only Tubificidae known from India were represented by four species, each belonging to a different genus. Besides *Limnodrilus socialis* and *Branchiura sowerbyi* there were only two other rather rare species, *Bothrioneuron iris* Beddard and *Monopylephorus parvus* Ditlevsen. In a paper just published (15) Stephenson has announced the discovery of *Tubifex tubifex* and *Aulodrilus remex* in that country. It appears that *Tubifex*, which is a common European Tubificid, is rare in India and probably in the East. The species described in the present paper belong to the genus *Aulodrilus*, which is at present the least known genus of the Tubificidae. This genus was established by Bretscher (4) in 1899 for *A. limnobius* in Switzerland.

\* Communicated by Dr. J. STEPHENSON, F.Z.S.

† For explanation of the Plates, see p. 969.

He places it as an appendix to the Tubificidæ, though he thinks that it fits neither with that family nor with the Lumbriculidæ, and suspects that it may be necessary to found a new family for it. Piguet (11) described a second species in 1906 and placed it among the Naididæ as *Naidium pleuriseta*; but later transferred it to *Aulodrilus*, which he considers to belong neither to the Tubificidæ nor to the Naididæ, as he saw retractile penes in front of the ventral setæ of segment 7. He did not complete the study of the worm, and so could not be sure about its position. Stephenson in a paper (15) published in 1921 describes another species, *A. remex*, from India as above-mentioned.

The genus, which hitherto has been characterized mainly by the character of the needle setæ (crotchets), is now well established, as will be seen from the following description. The genital organs, unknown to all the previous authors, are described at full length in the present paper and decide the position of the genus in the family Tubificidæ. The fact that the needle setæ possess a small outer prong (the one on the outer side of the curve of the shaft), which is not the usual condition in the Microdrili, is not of very great generic importance, because in some Tubificids, e. g. in *Tubifex velutinus* Grube, some crotchets of a similar kind are present; and moreover in *A. stephensoni* the outer small prong is missing altogether, the needle setæ being thus singly pointed and not forked.

The hinder end of the body is narrower and thinner, and does not show any signs of segmentation. Sometimes a faint indication of external segmentation may be visible, but the zone of budding lies some distance in front of the anus, where a large number of new segments are being formed. One can easily recognize the worm by its peculiar hinder end. This feature was previously described by Piguet in *A. pleuriseta*, and Stephenson has recently confirmed it in *A. remex*, and remarks "the most posterior region shows no proliferation, nor even any segmentation, but there is a zone of proliferation and formation of numerous new segments some little distance in front of the anus." Later on, he adds "such a budding zone as that of the present genus is so far as I know unique."

*Aulodrilus* connects the genera *Branchiura*, *Kawamuria*, *Psammocytes*, and *Tubifex*; it also shows some resemblance to *Monopylephorus africanus* Michaelsen in the points that it possesses a spermiducal chamber, penial setæ and spermathecae in the 9th segment. In certain points it also bears some similarity to the Naididæ. One point of similarity, namely the anterior position of the genital organs, is however merely a case of extreme variation within the genus *Aulodrilus* and hence not of any generic importance. This follows from the description here given of a second species, undoubtedly belonging to this genus, in which the reproductive organs lie in the usual position for the Tubificidæ. That it is a Tubificid is beyond any doubt, but it shows a greater simplicity of structure than any other genus of the family.

It is remarkable that the atrium here is situated far forwards, and is followed by a convoluted tube of great length which is enclosed in a thick covering of muscle fibres forming a structure somewhat similar to that of the cœlomic sac in *Branchiura* and *Kawamuria*. I have called the tube following the atrium and enclosed in the cœlomic sac the "atrial duct" and restricted the term atrium to the anterior rounded portion into which the prostate opens. The use of the muscle fibres forming the cœlomic sac, or better the muscular sac, is to evert the terminal part of the atrial duct, which thus projects out of the "spermiducal chamber" as a fairly long pseudo-penis.

The term "spermiducal chamber" used by Goodrich in the case of *Vermicululus* is retained here too, for a similar structure, *i.e.* the ventral depression of the body-wall, into which the atrial ducts open and the penial setæ lie.

The prostate gland as usual in the family is voluminous and composed of cells, which when full of secretion become disorganized and lose their cellular structure, the secretion being thus massed together flows directly into the atrium. The prostate appears to arise as a part of the atrial epithelium, which bursts out of the atrium as a sort of hernia or outgrowth.

The penial setal sacs are provided with masses of large pear-shaped gland cells, which lie in the body-cavity outside the setal sacs themselves though connected with their walls.

I wish to express my warmest thanks to Mr. F. A. Potts and Dr. J. Stephenson of Edinburgh for valuable suggestions in connection with this work.

## (2) DIAGNOSIS OF THE GENUS AND SPECIES.

The chief characters of *Aulodrilus* are the following:—Dorsal setæ capilliform; uncinata or oar-shaped (with thin flattened distal extremity); ventral setæ uncinata. The uncinata setæ (crotchets) have the outer prong (the one on the outer side of the curve of the shaft) much smaller than the inner, or the outer prong may be absent. The penial setæ, of very different form, are the modified ventral setæ of the 7th or 10th segment. The atrium is small and subspherical; it is followed by a long convoluted atrial duct, which is enclosed by a thick covering of muscle fibres to form the "muscular" or "cœlomic sac." The terminal part of the atrial duct is capable of being evaginated to form a long soft pseudo-penis. The sperm-sac is formed by the backward extension of septum 6/7 or 9/10, and the ovisac by that of septum 7/8 or 10/11. The clitellum occupies segments 7 and 8, or 10 and 11. The spermathecae lie in segment 6 or 9. The hearts are in segment 6 or 8. Supra-intestinal, sub-intestinal, and integumental capillary networks are absent. The formation of new segments takes place some distance in front of the anus. Asexual reproduction by fission as in the Naididæ does not take place.



*Aulodrilus kashi* resembles *A. remex* in possessing somewhat similar oar-shaped setæ in addition to the ordinary needles; but its hair setæ are longer than the needles. The first nephridium lies in the 11th or 12th segment. It is twice as long as *A. remex*. The genital organs are in segments 6 and 7, the clitellum is on segments 7 and 8, and spermathecae are in the 6th segment; the spermiducal chamber occupies segment 7.

In *A. stephensoni* there are no oar-shaped needles, in which point it markedly differs from the above species. The needles are here singly pointed and not forked—a point in which it differs from all the other species. The genital organs here lie in segments 9 and 10, the clitellum extends over segments 10 and 11 and the spermathecae are in segment 9. The penial setæ are the modified ventral setæ of the 10th segment.

(3) *AULODRILUS KASHI*, sp. n.

(a) *Habits and External Characters.*

The worms live invariably in tubes formed of small foreign particles of sand and debris cemented together with mucus secreted by the glands in the skin; in the undisturbed condition the posterior portion generally remains outside the tube in the water, and is waved gently to and fro somewhat like the tail of *Tubifex*, *Limnodrilus*, and other Tubificids, while the anterior end and greater portion of the body remains buried in the tubes inside the mud. On being disturbed, however, the worms withdraw their freely moving tails with fair rapidity. When placed isolated in water, they do not come out of the tubes very readily, but when after a few minutes they do come out, they move like other Tubificids.

About 40 specimens of this form were obtained between February and April, of which 27 were sexually mature. They vary from 20–28 mm. in length and hence are much larger than *A. remex*. The hinder end of the worm is much thinner, the diameter being .13 mm. The diameter near the anterior end is .26 mm. The colour is yellowish-red due to the blood seen through the transparent body-wall.

The prostomium is bluntly conical, about  $90\mu$  in length. The number of segments varies from 31–70, plus a considerable number of undifferentiated new segments, followed by a narrow terminal region of about .78 mm. in length, which does not show any sign of segmentation (Pl. III. fig. 11). The number of new segments forming in the region of budding varies considerably, but it usually is large. The small narrow region behind the zone of proliferation and in front of the wide terminal anus Piguët regards as physiologically a gill. According to him it possesses a rich cutaneous vascular plexus, but this I have not been able to observe in my specimens. The anus can dilate during life, forming what Piguët calls a “branchial fossa.” The anus is wide



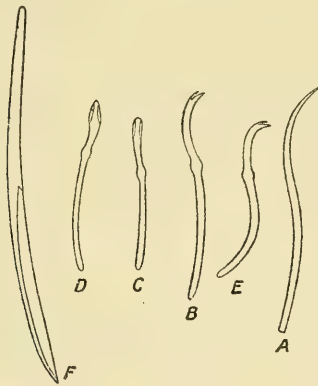
and terminal. The worms do not reproduce asexually by budding.

*Setæ*.—The setæ of both the dorsal and ventral bundles begin in the second segment, and are absent in a number of developing segments in front of the hinder end of the body.

There are three kinds of setæ in the dorsal bundles: capilliform, slightly hooked and doubly forked needles of the sigmoid type, and oar-shaped setæ with somewhat flattened or fan-shaped distal extremity, which sometimes may end in a fine point. The number of setæ in a dorsal bundle varies from 8–10 of which 2–4 may be capilliform; these are generally absent in the first two or three setigerous segments, and hence begin in the 4th or 5th segment.

A hair seta (text-fig. 1, A) is 99–104  $\mu$  in length, always

Text-figure 1.



A. Hair seta; B. Uncinate seta of a dorsal bundle; C and D. Dorsal setæ flattened near the distal end (oar shaped); E. Uncinate seta of posterior ventral bundle; F. Penial seta.  $\times 540$ .

longer but more slender than the needle. It is nearly straight with a slight sickle-shaped curve and tapers to a fine point. The needles of the ordinary kind (text-fig. 1, B) are, as usual, doubly curved and slightly hooked at the distal extremity, which is forked. In length this seta varies from 75–92  $\mu$ ; it bears a swelling or nodulus, which is situated much nearer the distal extremity, the proportions of the distances from it to the proximal and distal ends being about 2 : 1. The prong on the outer side of the curve of the shaft is smaller and much narrower than the one on the inner side, appearing as fine as a line or a denticle; in some preparations it may be broken off, and then the seta appears as a single pointed needle. The dorsal setæ of the third kind (text-fig. 1, C and D) are flattened at the distal extremity and appear oar-like. They

resemble the webbed setæ described by Lankester in *Tubifex*, but for the prongs at the sides of the web. The distal end may be either rounded or bluntly pointed. Their length as measured in two specimens is  $66-69\ \mu$  in one and  $78-80\ \mu$  in the other; the nodulus here also is situated near the distal extremity, the proportions of the distances proximal and distal to it being 2:1 as in the ordinary needles. The oar-shaped needles are less numerous and are often found in the segments in front of the middle of the body (in *A. remex* these setæ begin in segment 13 in one specimen and 7 in another, but they continue to the hinder end of the body). The thin flattened distal end shows comparatively faintly, is marked by one or two vertical lines and has not the distinct outline of the rest of the shaft.

The ventral setæ (text-fig. 1, E) are, generally speaking, similar to the forked needles of the dorsal bundles. The inner prong is much broader, about four times as thick or even more than the outer one, which looks like a fine process and in length may be as long as or slightly shorter than the inner one. The shaft of the seta in the posterior part of the body is shorter and more strongly curved than in the anterior part. In the anterior part of the body their length is  $90-100\ \mu$ , in the posterior  $60-70\ \mu$ . The nodulus is situated here also much nearer the distal end, the proportions being—the distance proximal to nodulus: distance distal to nodulus: 3:2 in the setæ in the anterior part, and about 2:1 in those of the posterior part of the body.

The penial setæ are always present during the sexual phase, and in this species are the modified ventral setæ of the 7th segment. They lie (Pl. I. fig. 1) inside the spermiducal chamber and posterior to the openings of the atrial (ejaculatory) ducts. In one specimen the penial setæ occupied a position anterior to these openings. Their number is 1-3, generally 2 per bundle. Their length is about  $\cdot 25$  mm. The form of the seta (text-fig. 1, F) is very different from that of any of the dorsal or ventral setæ. The shaft is slightly curved and is somewhat broadened in its distal portion; its tip comes to a fine point and looks somewhat like the end of a spear. The distal portion has a blade-like inner edge and an outer narrow thick border, which is continuous with the thick proximal part. There is a narrow longitudinal depression on one face of the blade, which gives it to some extent the appearance of a spoon. The breadth at the base of the shaft is about  $7\ \mu$ , while at the distal expanded portion near the tip it is about  $12\ \mu$ .

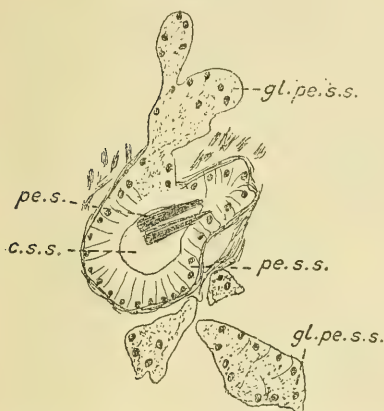
#### (b) *Internal Anatomy.*

The cuticle lines the spermiducal chamber, which is therefore to be considered as a depression of the ventral body-wall. Large mucous cells are a prominent feature of the surface epithelium; these no doubt secrete the mucus, which with the addition of foreign particles forms the tube of the worm. The cells of the

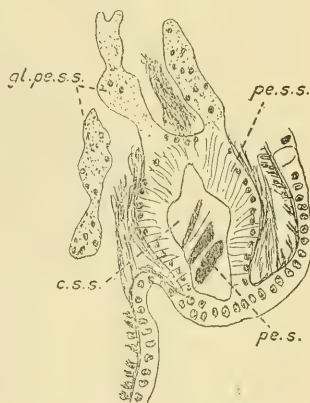
lateral line are small, about 15 by 6–9  $\mu$  in size, have an irregular form and contain a conspicuous rounded nucleus of 4  $\mu$  diameter; they are only 4–5 in number in each transverse section.

The clitellum extends over segments 7 and 8, which contain the principal genital organs; it leaves free the area on the ventral surface occupied by the spermiducal chamber (Pl. I. fig. 4). It is opaque white in appearance and merges gradually into the epidermis in front and behind. Its cells are about 70  $\mu$  in height, *i. e.*, about four times as high as the ordinary epidermal cells. In the clitellar cells the cell outlines are lost, and the nuclei disappear, though these may be visible in the early condition lying here and there near the inner border. The cells have a coarse granular appearance; the mucous gland cells are present in the clitellum also.

Text-fig. 2 A.



Text-fig. 2 B.



Vertical sections through the penial setal sac and the glandular masses in connection with it in two different specimens. The penial seta is rooted in the wall of the setal sac.  $\times 390$ .

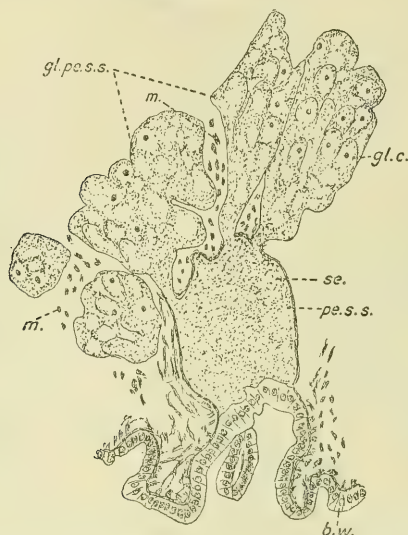
[For explanation of letters used in the figures, see p. 969.]

*Setal Sacs.*—In the sexual phase the ventral setal sac of segment 7, which contains the penial setæ, is nearly circular in outline as seen in a transverse section of the body (Pl. I. fig. 2). Its wall consists of tall columnar epithelial cells of about 18 by 2.5  $\mu$  size, containing a few nuclei near the outer periphery; outside the epithelium there is a thin layer of muscle fibres. Cell outlines are not recognizable in the greater portion of the penial setal sac, except for a small portion on its ventral surface, on account of the secretion, with which the cells seem to be filled; the nuclei are also mostly lost in this region (text-fig. 3), though they are easily recognized in the ventral portion of the wall, where the secretion is not present. The

setal sac is continued below as a tube to open externally, and is there lined by cells which have the same structure as those of the epidermis at the opening, out of which the penial setæ project.

A very obvious feature in the constitution of the penial setal sac is the presence of several conspicuous lobules of a glandular mass, which lie outside it in the body-cavity though connected with its wall (text-figs. 2 A & B and text-fig. 3 & Pl. I. fig. 2). The lobules vary in diameter generally, and each is continued at its narrow inner end into the wall of the setal sac. The various lobules are separated from one another by a few narrow bands of muscle fibres. The epithelial wall of the

Text-figure 3.



Vertical section through the penial setal sac of a specimen in a more advanced stage of maturity. The glandular masses here are much bigger and lobed. The secretion of the gland cells is seen passing into the epithelial wall of the setal sac.  $\times 220$ .

setal sac, as has been pointed out, does not show any cell outlines for the greater part (text-fig. 3), and this is specially the case where the lobules pass into it, but is filled with a coagulum, which is as a matter of fact the secretion. It seems to me that the secretion of the gland cells which constitute the various lobular masses passes into the epithelial cells and is thus stored up there; it is also likely that the epithelial cells are capable of secreting too. Each penial seta is rooted only in the innermost portion of the wall of the sac. The whole structure and appearance of the glandular masses and their connection with the epithelium of the setal sac resembles a somewhat similar condition



shown by the prostate and the atrium in these worms, as we shall see later. That the epithelial cells of the setal sac, filled with secretion generally lose their cellular structure, except in the small ventral portion, which is continuous externally with the outer tubular part of the sac and not being connected with the glandular cells is hence devoid of secretion, can be easily followed in sections.

Each glandular mass consists of a number of somewhat elongated pear-shaped cells closely pressed together. The cells have a frothy appearance on account of the secretion they are filled with, have mostly lost their cellular outlines, are deeply stained with hæmatoxylin or similar stains, and are similar to those of the prostate; only a few nuclei are present and all this tends to show that after secreting they lose their structure.

The septa are thin throughout the body. The first septum lies between the third and fourth segments.

*Alimentary canal.*—The buccal cavity is capable of extrusion; the epithelial cells lining it are devoid of cilia. The pharynx occupies segments 2 and 3, and is covered over by a small amount of chlorogogen pigment; its wall is folded so that about 3–4 diverticula which may be again divided into two arise from it; in one case a fairly long diverticulum arising from the anterior part ran independently for some distance and then opened into its posterior part. The pharyngeal epithelium is composed of high columnar cells with nuclei about the middle of their length, and provided with cilia of large size, which arising from the opposite walls meet in the somewhat narrow lumen of some of the diverticula. In a few specimens having a more slender body the pharynx was not folded, but here the cells of the dorsal wall, about 45–70  $\mu$  in height formed a sort of disc-like structure projecting into the pharyngeal cavity, which consequently appeared of a somewhat crescentic form. The cells lining the ventral portion of the wall here were only 27–36  $\mu$  in height and 4.5  $\mu$  in breadth. Outside the pharyngeal epithelium lies a fine layer of circular muscle fibres, from which fine strands of muscles arise here and there, specially on the dorsal and lateral sides and connect it with the body-wall.

The pharyngeal gland cells lie in groups separated by the muscle strands, which form a sort of loose network around them and largely fill up the body-cavity of the pharyngeal region. Each gland cell takes a deeper hæmatoxylin stain than the rest of the tissues; it consists of a broad outer expanded portion in which lies the nucleus with the nucleolus and a long inner narrow portion, which can be easily mistaken for a connective tissue or a fine muscle fibre. The cell groups surround each of the pharyngeal diverticula referred to before. In sections most of the gland cells are cut in such a way that their long inner stalks become completely separated off from their outer expanded portions and look like fibres. Hence arises a difficulty in tracing the cells to their inner ends. That the fine stalks of the gland cells reach



the fine basal membrane surrounding the pharyngeal epithelium is beyond doubt, and whether they penetrate the epithelium lying in between the cells to open into the lumen I have not been able to see. The pharyngeal gland cells extend also behind the pharynx and lie in masses of a somewhat irregular kind in the body-cavity near the first septum; I believe that these also send processes to the alimentary canal. The œsophagus occupies segments 4-8 and differs from the intestine in its lesser diameter. The epithelium is separated from the surrounding layer of muscle fibres by a fairly continuous sinus, which is interrupted at a few places by the epithelial cells meeting the muscular layer. The œsophagus suddenly dilates about the middle of the 8th or the beginning of the 9th segment to form the intestine, which in structure corresponds to the œsophagus; it occupies most of the available space in the segment and is attached to the body-wall by muscular strands.

A large number of parasites belonging to the group Ciliata Astomata (Pl. III. fig. 12) were found in the intestine of the majority of the specimens.

*Blood vascular system.*—The blood is yellowish-red in colour and devoid of corpuscles. The dorsal and ventral blood-vessels are the only longitudinal trunks present, and they are connected with each other by a pair of commissural vessels in every segment. The dorsal vessel is contractile and extends throughout the length of the body; it occupies a dorsal position only in the first six segments, after which it turns to lie ventrally on the left side near the ventral blood-vessel. The ventral vessel divides in the first segment to form a pair of slightly coiled vessels which unite above to form the dorsal vessel. The peri-visceral vessels are large and undulating; they lie in the posterior part of the segment in front of the septum. In the region of the pharynx they form a series of loops around it; in the posterior portion of the body they lie very close to the body-wall and make it appear vascular, but they do not branch to form such a cutaneous plexus as is present in some of the Tubificids. In the 6th segment the dorsal vessel communicates with the ventral vessel by a pair of short lateral hearts. The intestine also is surrounded by a sinus, which lies outside the gut epithelium and is interrupted at a few places by the epithelial cells touching the muscular layer outside; it is directly connected with the dorsal vessel by means of a short vessel once in each segment. The dorsal vessel is usually enlarged in the 7th segment, where it turns on the left side; the peri-visceral vessels in the region of the sperm and ovisacs become enlarged in the sexual phase and lie coiled round them. The absence of supra-intestinal and sub-intestinal vessels as well as the parietal network indicates the simple condition of the vascular system, which is emphasized by the presence of a fairly continuous peri-intestinal sinus as in the Naididæ. The vascular system therefore is much simpler than that of *Tubifex*, *Ilyodrilus*, and *Branchiura*.

*Nephridia*.—The nephridia are constructed on the same plan as in *Tubifex*. They are unpaired and lie on one side of the body near the ventral surface close to the ventral blood-vessel. The nephrostome is followed by a short uncoiled tubular portion with thin walls, which after piercing the intervening septum undergoes several windings, before it becomes continuous with the convoluted tube of the glandular mass. A small pear-shaped enlargement of the tube before it passes into the glandular mass is seen only in sections with some difficulty. The tube in the glandular mass is coiled two or three times to form well-marked loops; it then emerges as a somewhat wider tube with thin walls, on ventral side nearer the anterior end of the nephridium, and not at the posterior end as in *Tubifex*. The terminal free portion of the tube is short and expands near the distal end to form a small vesicle, which opens to the exterior at the nephridiopore, a short distance in front of the ventral setæ. The first nephridium lies in the 11th or 12th segment, after which it is present regularly in every segment, except in the terminal portion of the body.

*Nervous system*.—The cerebral ganglion is deeply cleft in front, slightly so behind. The median lobe, which characterizes the brain of *Tubifex* and other Tubificids is here absent, but a median nerve is given off anteriorly to the prostomium. The peri-pharyngeal cords unite in the 2nd segment to form the first ganglion of the ventral nerve-cord. The giant nerve fibres so characteristic of the nerve-cord in the Tubificidæ are absent here.

*Genital organs*.—I collected on several occasions between the middle of February and the end of April a few specimens having these organs at various stages of maturity. The genital organs are placed far more anteriorly than in any other Tubificid, *i. e.* in segments 6 and 7; in other Tubificidæ they are never present in front of the 9th segment except in *Tubifex (Ilyodrilus) bedoti*, where they lie in segments 8 and 9. In this respect *Aulodrilus kashi* comes near the family Naididæ, in which the sexual organs lie in segments 5 and 6. The gonads are the first organs to appear when the period of sexual maturity sets in. In one specimen only testes were present; on the other hand where the sexual organs were fairly advanced, the testes had entirely disappeared, having given rise to an enormous mass of developing sperms, which filled the 6th segment and the sperm-sac. The ovaries are always present till the latest stage of maturity and are quite large, as in other Tubificids.

The testes are ovoid masses, one on each side, attached by a narrow base to the posterior face of septum 5/6 near the ventral body-wall.

The ovaries in a stage of advanced maturity are a pair of large massive organs of a somewhat ovoid or irregular form with a small basal stalk, by which they are attached to the posterior face of septum 6/7 near the ventral parietes. They remain throughout the sexual phase, even when the ovisac is filled with ova and

yolky substance—a feature which distinguishes the Tubificidæ from the Naididæ, in which the ovaries disappear early like the testes. Each well-developed ovary measures about  $\cdot 088$  mm. in height and  $\cdot 095$  mm. in breadth; it extends as far back as the celomic sac which lies in the hinder part of the segment. It is composed of ova at various stages of maturity, somewhat loosely arranged and not consolidated as in the Megadrili, and a large mass of yolk. The yolk generally fills up a large space in the centre of the ovary, while the ova lie all around it forming the periphery; in two cases, however, the yolk extended on the upper border, and the ova were lying then on the anterior, ventral and posterior margins. It seems probable that only the cells around the periphery of the ovary develop into ova, and that the central cells break up, lose their individuality and form the large amount of yolk-matter. The developing oocytes, when of sufficiently large size get discharged with a part of the yolk and find their way into the ovisac, where they complete their further growth.

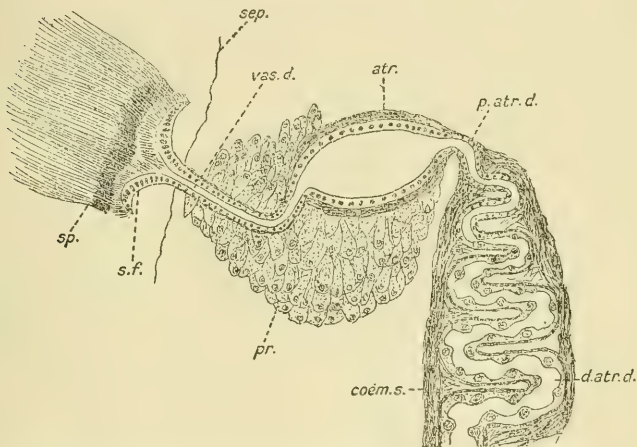
There are no special blood-vessels for the ovary, or any part of the genital apparatus; the peri-visceral blood-vessels and the dorsal vessel become much enlarged in the region of the body containing them.

The vas deferens lies in the 7th segment, and opens internally by a large seminal funnel in the segment in front, piercing septum 6/7; it opens externally in a large ventral depression of the body-wall—the spermiducal chamber. Each duct lies in two segments and consists of the following parts: the seminal funnel, the vas deferens proper, the atrium with the prostate and the atrial duct, which is very long, much coiled and enclosed in a thick coat of muscle fibres to form a spherical or ovoid muscular or celomic sac.

The seminal funnels are situated in the 6th segment—*i. e.* the segment in front of that in which the tube itself lies, near the ventral parietes, projecting freely and lying in front of the lower part of septum 6/7, below the opening of the sperm-sac (text-fig. 4). Each funnel about  $75\mu$  in height is cup-shaped with everted lips; in an advanced stage it is wide and shallow reaching about  $75\mu$  in breadth. It is lined by a single layer of columnar ciliated cells of  $20\text{--}28\mu$  height except near the margin of the upper lip, where the height is somewhat less; the cells are about  $3\text{--}6\mu$  broad, are wider on their inner ciliated border and narrower, appearing somewhat fibre-like at their outer end. The epithelial cells contain large oval nuclei,  $5\text{--}6\mu$  in greatest diameter placed about middle of their length; the nuclei are somewhat smaller in the lower marginal cells of the funnel. The cilia are fairly conspicuous. The peritoneal layer does not appear to be present outside the funnel epithelium. The elongated sperm-heads of  $11\text{--}12\cdot 6\mu$  length with the tails about four times in length lying behind form a regularly arranged dense mass near the funnel opening (text-fig. 4). The lower lip of the funnel lies near the ventral parietes, about  $32\mu$  distance from it.

The vas deferens is a short slightly curved tube leading back from the seminal funnel and opening behind into the anterior end near the ventral margin of a somewhat swollen chamber, the atrium. The duct is circular in transverse section, and of nearly the same breadth throughout, *i. e.* about  $25\ \mu$ . The lumen is only  $4\ \mu$  in diameter. It is lined by cubical epithelial cells of  $7.5\ \mu$  height and without definite cell-outlines; the oval nuclei of  $7.5\ \mu$  greatest diameter lie at right angles to the height of the cells. Outside the epithelium there is present a thin layer of circular muscle fibres, which as the seminal duct joins the atrium becomes much thicker and is continued into the thick muscular coat of the atrium. A few nuclei seen in sections here and there outside the muscular layer indicate the presence of the peritoneal layer.

Text-figure 4.



Semi-diagrammatic vertical section of the vas deferens apparatus as compiled from several successive sections.  $\times$  ca. 540.

In the early stage the vas deferens is shorter and runs nearly straight to open at the anterior end of the atrium; it is also narrower, the breadth then being only about  $14\ \mu$  including a lumen of  $2.5\ \mu$ . The epithelial cells are cubical, the muscular coat around the epithelium is feebly developed or even in a still earlier stage absent. The epithelial cells of the vas deferens are altogether devoid of cilia, while in the case of *Tubifex tubifex* and *Limnodrilus claparèdeianus* the cilia are quite conspicuous. In the latter genus I had the opportunity of examining the vas deferens on several occasions and found the epithelium provided with long cilia arising from the basal granules, which are visible in the living worm under a high power. It is also interesting to note here, that the vas deferens throughout the sexual phase is short.



What corresponds to the atrium in other forms is a long tubular structure consisting of three parts. The first part, that into which the vas deferens opens, is a dilated chamber, ovoid in form, to which I restrict the term atrium; and the rest of the tube I call the atrial duct. This is much convoluted and enclosed in a thick sheath of muscle fibres which form a chamber—the cœlomic or muscular sac. The atrium has its long axis parallel to that of the body (Pl. I. fig. 3, text-fig. 4; and Pl. II. figs. 5, 6, & 7); in a fully mature form it is about  $143\ \mu$  in height,  $92\text{--}114\ \mu$  in breadth and  $192\ \mu$  or about  $\frac{1}{5}$  mm. in length; in the posterior portion however, its height is only about  $74\ \mu$ . Its wall consists of a muscular sheath of  $5\text{--}7\ \mu$  thickness, which is surrounded externally by a thin layer of peritoneum; and of the inner epithelium, which in many of the specimens approaching advanced sexual maturity loses its cellular character, appears simply frothy and stains like the coagulum with which the atrial cavity is filled. Though the cells have lost their structural features and nuclei, it can be recognized that they have increased in size. The cells lining the hindmost part of the atrium retain, however, their columnar outlines and their nuclei. The secretion of the larger, anterior portion of the atrium appears to be similar to that of the prostate cells.

Prostate.—The prostate gland is characteristic of the Tubificidæ among the Microdrili.

Connected with the atrium on its ventral side nearer its rounded anterior end there lies a voluminous mass of gland cells, which surrounds it, and a greater portion of the vas deferens in front; it has the form of an irregularly shaped lobate mass, sometimes reaching as far back as the cœlomic sac. The mass lies dorsally to the ovary, which occupies a ventral position in this region of the body (Pl. I. fig. 3). The cells are large and pear-shaped with the nuclei contained in the outer swollen portion; their narrow inner portions or fine ductules lie near the centre of the gland (Pl. II. fig. 5) and converge towards the point where the prostate is in communication with the atrium, while the broad outer portions of the cells lie towards the periphery. When the prostate is fairly well developed, which was the case in most of the specimens under examination, the ductules or the inner portions of the cells lose their entity and become more or less disorganized; and in the period of more advanced maturity, the outer portions of the cells become more or less dissolved, and the cellular structure disappears, only a few nuclei being left here and there. As the cells lose more and more in structure, the secretion becomes collected in a mass and passes straight into the atrium, where the prostate is connected with it (Pl. II. figs. 6 & 7). The prostate communicates with the atrium by an opening  $42\ \mu$  wide; here both the muscular and epithelial layers of the atrial wall are absent, so that the prostate appears to arise as an outgrowth of the atrial epithelium. In the mature worm the atrial



epithelium is thus replaced by a mass of secretion, which has apparently originated in the prostate. Vejdovsky (16), who studied the development of the atrium and the prostate has stated that the latter is formed by the proliferation of the cells of the lining epithelium of the atrium at a point, where the muscular and peritoneal layers are interrupted, so that the prostate cells and those of the atrial epithelium are intimately connected with one another; this agrees very well with what I find in sexually mature specimens. Though I am not in a position to say anything at present as to the origin of the prostate, its connection with the atrium certainly suggests its origin from the latter. It is, however, clear beyond doubt that the prostate cells become disorganized when full of secretion, especially in their long inner ductule-like portions, and the secretion is discharged mechanically as a stream of inwardly moving fluid running through the centre of the glandular mass into the atrial cavity at the point of communication.

Muscular or celomic sac.—The atrium is followed by a narrow duct of about the same diameter as the vas deferens, which after a short length of about  $22\mu$  undergoes a few irregular windings and may be called the proximal portion of the atrial duct (or the middle portion of the atrium, if it is regarded as a part of the atrium itself). It is continued into a longer and much wider terminal part, which also undergoes several windings, fairly regularly arranged one below the other, till it passes vertically downwards to open into the spermiducal chamber. The convoluted middle and distal regions of the atrium which constitute the atrial duct are bound up together and enclosed by a thick coat of muscle fibres so to form an ovoid structure, somewhat similar to the celomic sac of *Branchiura* and *Kawamuria*; the muscle fibres forming its walls are not compactly arranged, but somewhat loosely connected, so that there are left some narrow spaces here and there in between the strands of fibres, which have a few nuclei at certain places. The muscular sac extends ventrally as far as the spermiducal chamber; the muscle fibres forming the wall are continued in places as strands above and below into the musculature of the adjacent body-wall, where they pass through the layer of longitudinal muscle fibres to reach the layer of circular muscle fibres, and thus attach the sac to the body-wall. The height of the sac varies ordinarily from  $182\mu$  to  $240\mu$ ; in a specimen of smaller size it was  $125.5\mu$ ; its breadth varies from  $115$ – $182\mu$ . The narrow proximal portion of the atrial duct is  $14$ – $17\mu$  in diameter, having a lumen circular in transverse section with a diameter of about  $5\mu$ ; it occupies the topmost portion of the muscular sac, in front of which it leads out from the atrium. It is lined by cubical cells of size  $1$  by  $3\mu$  with conspicuous nuclei, but no definite outlines; outside it there is a thin layer of circular muscle fibres, which is continuous in front with the thick muscular wall of the atrium.

The epithelial cells of the wider distal portion of the atrial

duct are of a different appearance altogether. They are not of the same uniform height throughout, being tallest about the middle, where they are  $8.5\mu$  high; they are  $14.3\mu$  broad at the base; the inner portion of the cell projects into the lumen and contains the prominent rounded nucleus of  $3.5\mu$  diameter (text-fig. 4; Pl. II. figs. 6 & 7). The atrial duct in this region is much thicker than in the proximal part, being about  $28-40\mu$  in diameter as it gradually descends towards its termination: its lumen is  $16-22\mu$  wide. Outside the epithelium there is a covering of muscle fibres, which is slightly thicker than that of the proximal part of the duct owing to the presence of an additional layer of longitudinal muscle fibres external to the circular layer.

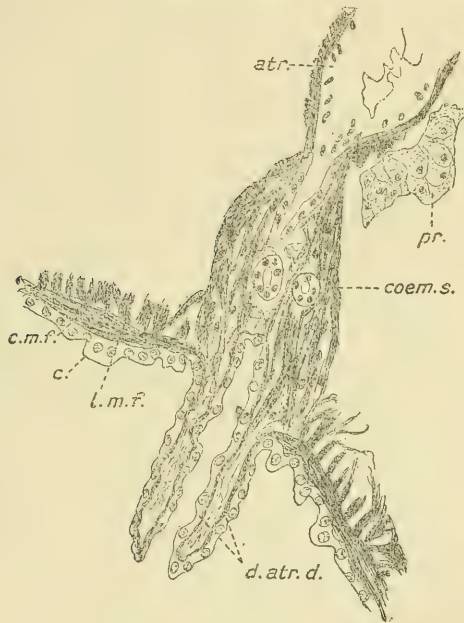
The paratrium, a blind tubular outgrowth of the atrium characteristic of *Branchiura*, *Kawamuraia*, and *Bothrioneuron* is here absent.

The spermiducal chamber is the median quadrangular depression on the ventral surface in the 7th segment formed as an invagination of the body-wall. The term has been used by Goodrich for a similar structure in *Vermiculus*. The chamber is large, about  $115\mu$  deep,  $200-250\mu$  long and about  $360\mu$  broad; the margin of its external opening is generally puckered. The openings of the atrial ducts lie inside at its anterior angles, one on each side, and in several specimens during life one or two penes were seen projecting out of it; sometimes, though rarely, the chamber is everted to form a papilla-like structure bearing the openings of the atrial ducts on its surface. The diameter of the terminal portion of the atrial duct near its opening is about  $32\mu$ , and the epithelial cells lining it gradually become of a uniform size, till they have the same form as those lining the inner wall of the chamber, which is the inturned epidermis. The cuticle of the epithelial lining of the chamber is continuous with that of the body-wall outside. The spermiducal chamber acts probably as a sort of sucker during copulation. Although there is no direct muscular mechanism for deepening the chamber, the radiating muscle fibres attaching the muscular sacs to the body-wall by contraction can indirectly pull it to a certain extent and thus deepen it to produce a sucker mechanism. The chamber was more deepened in the specimen in which the penis was protruded; and it appears that the contraction of the muscle fibres of the muscular sacs, which lie on its top, helps in deepening the chamber also.

Penis.—While examining several specimens in the living condition I saw in some cases one or two long cylindrical soft penes projecting out of the spermiducal chamber for a long or short distance. After proper fixation, sections were cut of two such specimens and the structure of the penis was investigated. This organ is covered externally by epithelium which is really the inner wall of the wide terminal portion of the atrial duct, and can be distinguished as such by the peculiar character of its cells, which

are high and low at regular intervals, and swollen at their inner projecting borders, which here lie outwards; the layer of muscle fibres outside the epithelium in the atrial duct forms here the inner wall (text-fig. 5). In the centre of the penis is a tube—a part of the atrial duct, the wall of which is continuous with that of the outer tube at the terminal opening. It is obvious therefore, that the penis is here formed by the eversion of the terminal portion of the atrial duct carrying with it the more proximal part as the central tube. The narrow proximal portion of the atrial duct does not seem to be drawn into the penis. The

Text-figure 5.



Part of transverse section of the body through the penis, coelomic sac, and a part of the atrium and prostate.  $\times 390$ .

eversion of the atrial duct is in all probability brought about by the contraction of the muscle fibres forming the muscular sac, which in turn are connected with the muscular layer of the body-wall. The penis in these worms is not a permanent structure and hence is very different from that in many Tubificids; it should be regarded as a pseudo-penis.

The sperm-sac is a median pouch formed by the extension backwards of septum 6/7; it opens anteriorly by a wide mouth in the 6th segment, and lies generally dorsal to the œsophagus in the 7th and a part of the 8th segments. Its walls are as thin as

the septum from which it is formed and consist of a thin layer of muscle fibres covered both on the inner and outer sides by a peritoneal layer of thin flattened cells. It is filled with sperms in various stages of development, and is in appearance and structure similar to the sperm-sac in the Naididæ.

A large portion of the body-cavity in the 6th segment is separated off laterally and ventrally from the smaller peripheral portion, contains all the organs belonging to the segment, and is filled with a huge mass of developing sperms. This part is surrounded by a wall, which is continued dorsally into the body-wall, its side walls become continuous ventrally to form the ventral portion of the wall, except at the ventro-lateral corners where the spermathecal ducts interrupt it as they pass out to their openings, and in the transverse sections of the worm here the peripheral chamber is thus divided up into a median ventral and two lateral parts (Pl. II. figs. 8 & 9). The wall which so separates the two portions of the body-cavity in the segment is composed of modified peritoneal layers, with a layer of circular muscle fibres in between. The outer peritoneal layer consists of branched cells of an irregular outline, the fibrillar branches given off from the various cells anastomose forming a sort of loose network, which with fairly big spaces enclosed in between gives the whole layer the appearance of parenchyma and is about five times as thick as the rest of the wall (Pl. III. fig. 10). The middle layer, consisting of circular muscle fibres, becomes continuous with the same layer of the ventral body-wall at the openings of the spermathecal ducts. The inner layer consists of cells fairly regularly arranged and not of the same breadth throughout, less regular on the lateral portions of the wall. This layer is continued dorsally into the peritoneal layer of the body-wall, which also in this segment may be parenchymatous in character, hence sometimes the whole peritoneal cavity, *i.e.* the space outside the wall of the central chamber, is filled with parenchymatous tissue formed by these peritoneal layers. The wall of the central chamber in the front and hinder parts of the segment gradually comes near the body-wall, and consequently the peripheral cavity becomes much more reduced; posteriorly it completely joins the body-wall about the level of the ventral setæ, in front of the seminal funnel; anteriorly it unites with the body-wall near septum 5/6, of which it appears to be a backward continuation, for in structure like the septum it is composed of three layers, the outer and inner peritoneal ones of more or less parenchymatous character with the middle one of muscle fibres. It seems clear that a good deal of support is afforded to the spermathecal ducts and proper protection to the developing sperms by this arrangement.

The anterior sperm-sac described in many Tubificids is here absent. The ovisac is formed as a pouch by the extension backwards of septum 7/8 and lies in segment 8, extending behind nearly to septum 8/9. It surrounds a part of the sperm-sac and extends



about  $\frac{1}{3}$  mm. distance behind it. It is filled with a large mass of yolk granules, and also contains a number of ova at various stages of maturity.

The female funnel is very small. Its posterior wall (the one nearer the septum behind) is represented by a patch of columnar epithelial cells of about  $25\mu$  by  $5\mu$  size lying on the anterior face of septum  $7/8$  near the ventral parietes, below the point where this septum is bulged backwards to form the ovisac. The anterior wall is, however, smaller and somewhat less conspicuous in sections. The epithelial cells of the funnel contain oval nuclei of  $2.5\mu$  diameter.

The oviduct is extremely short, about  $40\mu$  in length; it runs backwards and downwards somewhat obliquely to pass through the body-wall, through which it runs as a narrow irregular channel of about  $25\mu$  length and  $4\mu$  breadth. The female opening is wider at the inner margin of the epidermis and narrower at the outer.

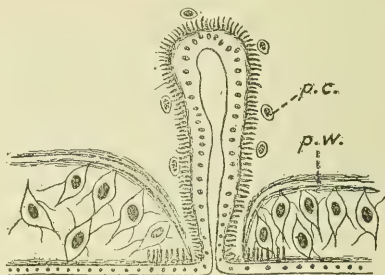
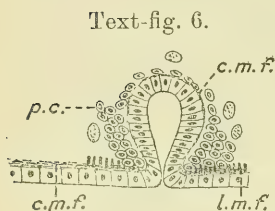
The spermathecae occupy segment 6; they lie freely for the greater part of their length in the central chamber of the body-cavity and are attached to the partition wall at the ventro-lateral corners as they pass downwards to their openings, which lie about the middle of the segment, much in front of the ventral setae. They are of considerable length and bent, so that each consists of two parts, a vertically elongated terminal portion—the duct, and an inner sac-like portion—the ampulla. The duct is not sharply marked off from the ampulla, but gradually passes into it. The ampulla is simple, and in the later stages of maturity quite large. The length of the spermatheca is  $234-305\mu$ . The duct is circular in transverse section, about  $88-133\mu$  in length and  $48.5\mu$  in diameter; in one case it measured  $175\mu$  in length. Its wall is  $17-20\mu$  thick, and is composed of an inner lining of columnar epithelial cells, surrounded by a coat of muscle fibres, with a thin layer of peritoneum outside. The epithelium is composed of a single layer of tall columnar cells of  $10-14\mu$  height and  $3\mu$  diameter, containing oval or somewhat elongated nuclei near the periphery, which lie with their long axis parallel to the height of the cells. The muscular sheath of  $2\mu$  thickness consists of an inner thin layer of circular muscle fibres and an outer thicker one of longitudinal muscle fibres. The peritoneum as usual consists of a layer of thin flattened cells with prominent nuclei. Near the opening the wall of the duct is less thick than in the upper part; the epithelial cells here are less tall, being nearly of the same height and form as those of the epidermal cells with which they are continuous; here the muscular coat is also thinner and is continued into that of the body-wall. The nuclei of the epithelial cells in the terminal part are not elongated, but somewhat rounded, and lie about the middle of the cell. The ampulla is much larger than the duct; its length varies considerably—in three specimens it was  $145$ ,  $185$ , and  $295\mu$ ; the maximum breadth was about  $120\mu$ . Its wall is much thinner than that of the duct,



but the three layers are recognizable. The epithelium consists of cubical cells of not more than  $6.5\mu$  height; in the advanced stages of sexual maturity the cells lining the inner blind portion are still lower, while those near the duct are somewhat square in outline. The muscular portion of the wall is much thinner, and consists of the same layers as in the duct. The thin peritoneum continuous with that of the duct forms the outermost layer. The greater thickness of the wall of the duct is due to the greater height of its epithelial cells and thickness of the muscle layers.

In one specimen the spermathecae were found to be in an early stage of development (text-fig. 6). Here it has the form of a small rounded chamber with an external opening and is not differentiated into duct and an ampulla. In size it measures  $120\mu$  by  $90\mu$ . Its epithelium is composed of tall cells with oval nuclei lying about the middle and is surrounded on each side by a mass of small peritoneal cells with prominent nuclei, a few of which are

Text-fig. 7.

Stages in the formation of a spermatheca.  $\times 840$ .

continued to form a thin layer above. There is no layer of muscle fibres present outside the epithelium, the cells of which have the same form and structure as those of the epidermis, with which they are continuous. In another specimen the spermathecae are better developed, and one of them was about  $160\mu$  by  $68\mu$  in size; here they have the form of an upright tube with an external opening. It is composed of columnar cells with conspicuous nuclei lying fairly near the periphery. Outside the epithelium a thin layer of circular muscle fibres surrounded by a few peritoneal cells is present, but the layer of longitudinal muscle fibres is not yet formed. The wall is  $22\mu$  thick and the lumen  $13\mu$  wide. Here also there is as yet no indication of the ampulla (text-fig. 7). The spermathecae thus arise as small rounded sacs by an invagination of the epidermis, then they assume a tubular form, but the differentiation into the duct and ampulla takes place much later. In both these cases there were no spermatozoa in the spermathecae.

## (4) AULODRILUS STEPHENSONI, sp. n.

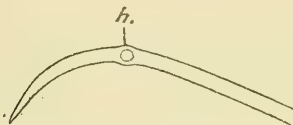
All the worms I obtained conform to the above description with the exception of one. This was first examined in the living condition and then studied from longitudinal sections. The description, though far from complete, gives the main features of the anatomy.

(a) *External Characters.*

The length is about 17.5 mm. The prostomium is bluntly conical. The number of segments is 56. The spermathecal openings lie on the ventral surface in the 9th segment much in front of the ventral setæ. The spermiducal chamber lies on the ventral surface of the 10th segment: as it is very shallow, the opening of the atrial duct is clearly seen in each of its anterolateral corners. During the examination of the living worm this chamber was not made out and the openings of the atrial ducts were supposed to be paired male openings; but the closer examination of the entire mount and subsequently the sections revealed the presence of the shallow chamber.

*Setæ.*—Dorsal and ventral setæ are present in all the segments from the 2nd segment backwards. The dorsal setæ are about 3–9 per bundle, each bundle being composed of 2–3 hair setæ, and 1–6 sigmoid needles. The uncinata seta (text-fig. 8) is about

Text-figure 8.



Uncinata seta of *A. stephensoni* as seen in balsam preparation of the entire specimen.  $\times 540$ .

half the size of the hair seta and ends in a fine point at the distal extremity. The small narrow outer process, or the distal prong which is present in the setæ of *A. kashi*, is not seen. It may be that its absence is due to breakage while making preparations. The nodule is situated at about one-third of the distance from the distal end, and the distal portion of the shaft beyond it projects outside the body-wall.

The ventral setæ are similar to the dorsal needles and are 7–10 in a bundle. The penial setæ are the modified setæ of the 10th segment and are 1–2 in a bundle; they lie in the spermiducal chamber slightly outside the opening of the atrial duct. In shape and length they appear like those of *A. kashi*; the breadth near the base is about 5–7  $\mu$ .

(b) *Internal Anatomy.*

The clitellum is twice as thick as the general epidermis and occupies segments 10 and 11.

The penial setal sac is large, rounded, about  $102\ \mu$  in diameter. Its wall is about  $30\ \mu$  thick and the lumen  $42\ \mu$  in diameter. In connection with the sac there is a large glandular mass similar in structure to that in *A. kashi*. The first septum lies between segments 3 and 4.

The pharynx extends up to the 4th segment, in which the oesophagus begins. The intestine commences in the 9th segment; it is larger till the 20th segment, after which it gradually narrows towards the posterior end, where again it slightly broadens, being stretched by a few muscle fibres, which attach it to the body-wall.

The dorsal and ventral blood-vessels are connected by an undulating commissural vessel in every segment. From the sections I have been able to find the position of hearts in segment 8.

The testes had disappeared, but a large mass of developing sperms fills up the central chamber of the 9th segment and the sperm-sac as in *A. kashi*. The structure and position of the seminal duct, prostate, atrium and muscular sac agree in essential respects with the description of these organs in *A. kashi*. The seminal funnel is cup-shaped with everted lips appearing somewhat like a thistle funnel; it is attached near the ventral parietes to the anterior face of septum 9/10 and lies in the 9th segment. The columnar epithelial cells lining it are  $14\text{--}20\ \mu$  in height. The vas deferens (text-fig. 9) is short and  $17\ \mu$  in diameter, its wall being  $6\ \mu$  thick; its lumen is  $5\text{--}6\ \mu$  in diameter; it is lined by cubical epithelial cells, which are covered by a thin layer of circular muscle fibres. The atrium is very much like that of the other species, but it is smaller, being  $80\ \mu$  by  $45.6\ \mu$  in size and lies here in the 10th segment. The cells lining the cavity have lost their cellular appearance owing to the secretion with which they are filled, and are surrounded by a thick muscular sheath.

The prostate is large and massive; it extends behind as far as the muscular sac. It is similar in structure to that in *A. kashi*, and opens here also into the antero-ventral border of the atrium.

The atrial duct (text-fig. 9) is much convoluted; it consists of proximal and distal portions, and is enclosed by a thick covering of muscle fibres which forms the muscular (coelomic) sac. The atrial duct as it leaves the atrium and before it enters the muscular sac is  $23\ \mu$  in diameter. Its lining epithelium consists of cubical cells, outside which there is a thin layer of circular muscle fibres. The proximal portion of the atrial duct is larger and has a wider lumen—about  $11\ \mu$ —than in *A. kashi*. The distal portion of the atrial duct is  $31\ \mu$  in diameter and is lined by an epithelium, which as in the other species is alternately

high and low. In the taller portions near the inner margin are the nuclei. The muscular sac is smaller in this species; it is about  $140\mu$  in length and  $114\mu$  in height.

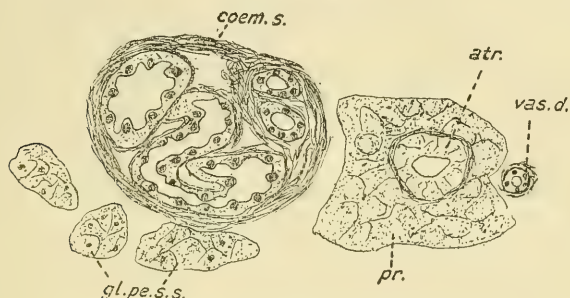
The sperm and ovisacs are formed here by extension backwards of septa 9/10 and 10/11 respectively.

The peripheral portion of the body-cavity in the 9th segment is separated here also by a partition as in *A. kashi*.

The ovaries are large and attached to the posterior face of septum 9/10 near the ventral parietes lying in the 10th segment.

The spermathecae lie in the 9th segment; in structure they are similar to those in the other species, except that the duct here is somewhat smaller.

Text-figure 9.



Longitudinal section through vas deferens apparatus of  
*Aulodrilus stephensoni*.  $\times 220$ .

The present species is principally distinguished from the former by the position of the genital organs, which here lie in segments 9 and 10. The seminal funnel lies in the 9th segment, while the rest of the efferent apparatus occupies the 10th segment. The sperm-sac and ovisac are formed by septa 9/10 and 10/11. The spermiducal chamber is very shallow and lies in segment 10. The uncinata setae are somewhat different from those of the other species, and the penial setae are the modified setae of the 10th segment.

##### (5) REMARKS ON THE SYSTEMATIC POSITION OF THESE WORMS.

It will be apparent from the above description that *Aulodrilus* must be referred to the family Tubificidae, although in *A. kashi* the anterior position of the genital organs, which lie here in segments 6 and 7, suggests a position closer to the Naididae, in which family these organs lie in segments 5 and 6. In *A. stephensoni* however, the sexual organs are present in segments 9 and 10, though in other structural details there does not seem to be any marked difference between the two species. This clearly decides the position of this genus in the Tubificidae. Another point, in which these worms resemble the Naididae, is the presence



of only one sperm-sac, which in appearance and structure is quite similar to that in the Naididæ; the anterior sperm-sac, which is present in many Tubificids is not present here. The main portion of the body-cavity in segment 6 or 9 is cut off from a peripheral portion, and forms the central chamber, which contains all the organs and is filled with the developing sperms—a peculiar feature of this genus. That the worms do not reproduce asexually by budding, which is a common occurrence in the Naididæ, separates them sharply from that family. There are, however, some features in which *Aulodrilus* shows a simplicity of structure comparable to that met with in the Naididæ, e.g. in the vascular system, where the presence of hearts in the 6th segment in *A. kashi*\* and the absence of supra- and sub-intestinal vessels and integumental network is noteworthy; the brain also is without a median lobe, and there are no giant nerve fibres in the ventral nerve-cord.

The distinct Tubificid characters are as follows:—

(1) Structure of efferent apparatus with an atrium and massive prostate followed by a long convoluted atrial duct enclosed in the muscular or cœlomic sac.

(2) Constant presence of a large ovary throughout the sexual phase.

(3) The large massive prostate is connected with the atrium as in *Tubifex* and some other Tubificids. It appears to be developed as an outgrowth of the atrial epithelium.

(4) Presence of a spermiducal chamber.

(5) Position of genital organs in *A. stephensoni* in segments 9 and 10.

(6) Penial setal sacs provided with large massive glands as in *Tubifex* (*Pelosclex*) *velutinus*. The penial setæ are also very long like those of the above species, and very different from the ventral setæ.

The anterior position of the genital organs in *A. kashi*, I think, is a character only of specific rank not showing in any direct way a closer relationship to the Naididæ, for in some genera such as *Megascolex* and *Buchholzia*† there are a few species in which the genital organs are placed one or more segments in front of those, which they generally occupy in the genus. In *Tubifex* (*Ilyodrilus*) *bedoti* the genital organs lie in the 8th and 9th segments and hence more anteriorly placed than in other members of the family. Among the Tubificidæ *Aulodrilus* seems to have relations on the one hand to genera *Tubifex*, *Ilyodrilus*, and *Psammoryctes*, and on the other to *Branchiura* and *Kawamuraia*. In possessing hair setæ, the long penial setæ and the massive glands in

\* In *A. limnobiis*, *A. pleuriseta*, and *A. remex* also the hearts lie in the 6th segment.

† In *Buchholzia appendiculata* Buchholz, these organs lie in the 7th and 8th segments, while in *B. fallax* Michaelsen, they occupy the usual position in the family, i.e., in segments 11 and 12.



connection with the setal sacs, and in the absence of the paratrium this genus resembles *Tubifex* and *Psammocytes*. But it differs from these genera in the following important points:—

- (1) Position of the zone of formation of new segments some distance in front of the anus.
- (2) Presence of a spermiducal chamber.
- (3) Presence of a muscular or cœlomic sac.
- (4) Variable position of genital organs.
- (5) Absence of spermatophores and a true penis.
- (6) Absence of supra-intestinal and parietal vessels.

In possessing hair setæ, an anterior atrium and a cœlomic sac, and in having no spermatophores, it bears a remarkable resemblance to *Branchiura* and *Kawamuraia*, the chief differences being the absence of a paratrium, the presence of penial setæ and a spermiducal chamber, and the absence of a true penis, which is said to be present in *Kawamuraia*.

*Aulodrilus* resembles *Monopylephorus africanus* Michaelsen, in possessing a spermiducal chamber, penial setæ, and spermathecae in the 9th segment, and in the absence of spermatophores and a paratrium.

The spermiducal chamber perhaps acts as a sucker during copulation. As this structure is present in *Monopylephorus*, which is however, in other respects very different from the present genus, I think this organ is correlated with the absence of a true penis and therefore probably is due to convergence in these genera.

#### (6) SUMMARY.

(1) The diagnostic characters of the genus and the species are given.

(2) The reproductive organs hitherto unknown are described in detail.

(3) The prostate is large and massive; it opens into the atrium near the antero-ventral margin. The prostate cells soon after they are functional and filled with secretion lose their structure and become disorganized, while the secretion passes as an inwardly moving mass into the atrium at the point where the gland is connected with it. The atrial epithelium also at this time undergoes a great change on account of the secretion by which its cells become replaced having lost their entity. The manner of connection of the prostate with the atrium suggests its origin as an outgrowth of the atrial epithelium.

(4) The cœlomic cavity in the segment which contains the spermathecae is separated off from the peripheral portion by the formation of a ventro-lateral wall, which is composed of a central muscular layer surrounded on either side by a peculiar parenchymatous tissue of peritoneal origin. The central chamber thus formed contains all the organs of the segment and is also filled with the developing sperms; the spermathecal ducts pass through the ventro-lateral corners of the wall on their way to the exterior.

(5) The spermathecae are ectodermal in origin, and arise as an invagination from the epidermis.

(6) As regards its systematic position *Aulodrilus* belongs to the Tubificidae, although it resembles the Naididae in some of its features. Among the Tubificidae it is related to *Tubifex* and *Psammocytes* on the one hand, and *Branchiura* and *Kawamuria* on the other. The spermiducal chamber, which is present in *Monopylephorus*, also seems to be independently derived in these genera, and perhaps acts as a sucker during copulation.

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## EXPLANATION OF THE PLATES.

*Explanation of Letters used in Figures.*

*a.* anus; *atr.* atrium; *ap.at.d.* aperture of atrial duct; *atr.d.* atrial duct; *b.v.* blood-vessel; *b.w.* body-wall; *c.* cuticle; *c.c.* central chamber; *cl.* clitellum; *cœm.s.* cœlomic (muscular) sac; *c.m.f.* layer of circular muscle fibres; *c.s.s.* cavity of setal sac; *d.b.v.* dorsal blood-vessel; *d.atr.d.* distal portion of atrial duct; *e.gl.c.* epidermal gland cell; *fem.f.* female funnel; *gl.c.* gland cell; *gl.pe.ss.* glands in connection with penial setal sac; *int.* intestine; *l.m.f.* layer of longitudinal muscle fibres; *l.p.w.* lateral portion of partition wall; *m.* muscles; *meg.n.* meganucleus; *n.* nodulus of seta; *o.* opening of vas deferens into atrium; *œs.* œsophagus; *ov.* ovary; *ovis.* ovisac; *p.atr.d.* proximal portion of atrial duct; *p.c.* peritoneal cells; *pe.s.* penial seta; *pe.s.s.* penial setal sac; *per.c.* peripheral chamber; *ph.* pharynx; *pr.* prostate; *pro.* prostomium; *pr.s.* prostate secretion; *prolif.* proliferating cells; *p.w.* partition wall; *s.* seta; *se.* secretion; *sep.* septum 6/7; *s.f.* seminal funnel; *sp.* sperms; *sp.ch.* spermiducal chamber; *sp.s.* sperm-sac; *sph.* spermatheca; *sph.op.* spermathecal opening; *v.n.c.* ventral nerve cord; *vas.d.* vas deferens; *v.b.v.* ventral blood-vessel; *v.p.w.* ventral portion of partition wall.

[Figs. 1-12 illustrate *Aulodrilus kashi* and fig. 13 *Aulodrilus stephensoni*.

All the figures except 1, 3, and 13 are drawn with camera lucida.]

- Fig. 1. Ventral view of anterior portion of the worm showing spermathecal openings in the 6th and spermiducal chamber in the 7th segment. Penial setæ and apertures of the atrial ducts lie in the spermiducal chamber.  $\times$  ca. 95.
- Fig. 2. Transverse section through the penial setal sac.  $\times$  220.
- Fig. 3. Semi-diagrammatic, compiled from several successive longitudinal sections showing the genital organs.  $\times$  ca. 120.
- Fig. 4. Transverse section of the body through the spermiducal chamber and its opening.  $\times$  120.
- Fig. 5. Transverse section showing the prostate opening into the atrium. The prostate and atrial epithelial cells have mostly lost cellular structure and are converted into the secretion.  $\times$  390.
- Figs. 6 & 7. Longitudinal sections through the prostate, atrium, and cœlomic sac. The prostate cells are disorganized, having lost their structure, and the secretion passes in a mass into the atrium. The atrial cells have also lost their entity, being replaced by the secretion.  $\times$  390.
- Figs. 8 & 9. Transverse sections in the spermathecal region. The cœlomic cavity in the 6th segment is divided by a partition wall into a central chamber and a peripheral portion. In fig. 8 one spermatheca is opening to the exterior.  $\times$  95.
- Fig. 10. A part of section in fig. 8 highly magnified. The partition wall consists of a circular layer of muscles in the middle with a layer of parenchymatous cells on either side.  $\times$  540.
- Fig. 11. Terminal portion of the body. The part just in front of the anus shows no signs of formation of new segments.  $\times$  97.
- Fig. 12. Ciliate astoma parasites.
- Fig. 13. Ventral view of a part of the body in *A. stephensoni* showing spermathecal openings in the 9th and shallow spermiducal chamber with penial setæ and openings of atrial ducts in the 10th segment.  $\times$  ca. 95.



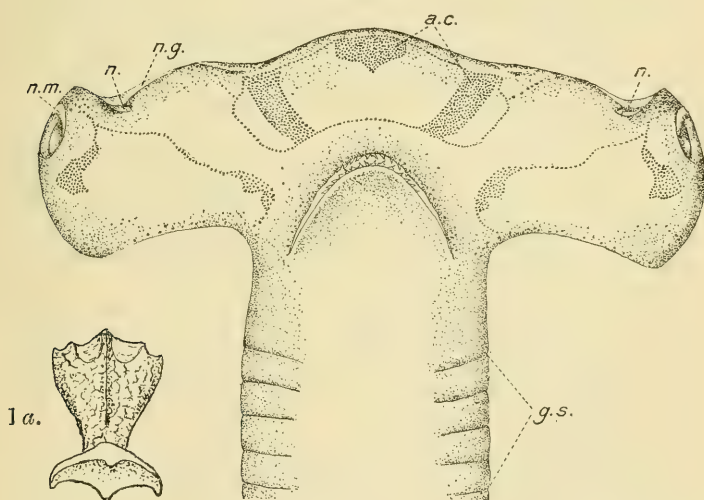
45. A Contribution to the Anatomy of a Hammerhead Shark (*Zygæna malleus* Shaw). By J. H. LLOYD, M.Sc. (Birm.), F.Z.S., and EDITH M. SHEPPARD, B.Sc. (Wales), F.Z.S., Zoological Department, University College, Cardiff.

[Received April 20, 1922: Read November 21, 1922.]

(Text-figures 1-7.)

The specimen on which this paper is based was given to us by Professor W. N. Parker, of University College, Cardiff, to whom our best thanks are due for his generosity. The specimen was sent to him some years ago by the late J. J. Neale, Esq., a local trawler owner, but unfortunately the fishermen had eviscerated it immediately after it was caught.

Text-figures 1 & 1 a.



Head in Ventral View.

a.c. ampullary canals.

g.s. gill slits.

n. nostril.

n.g. nasal groove.

n.m. nictitating membrane.

1 a. Dermal Dentine.

In this short paper we intend to include notes on the structure of the skull, brain, cranial nerves, and membranous labyrinth. Owing to the long immersion in spirit to which the specimen had been subjected the preparation of the skeleton proved to be a



matter of some difficulty, as the connective tissue had hardened to an extraordinary extent and the cartilage had become exceedingly brittle. We hope later to publish an account of the structure of the visceral arches, limb-girdles, vertebral column, and fins.

A description of this fish appears to be desirable as, with the exception of the external characters, we have not been able to find any consecutive account of its anatomy.

Both Garman (4) and Day (3) have given a species definition and figured the entire animal, the former including it in the genus *Cestracion* under the name of *Cestracion zygena* Linn. Gegenbaur (5) gives two figures of the head and briefly mentions the species in his text, but our observations do not agree with his in all respects. The macroscopic structure of the brain has been briefly described and figured by Busch (2) and Miklucho-Maclay (12).

#### SKULL.

The *cranium* bears at its anterior end a stout *rostrum* which consists of three bars. Two of these (*d.r.*) arise from the dorsal surface and run forward and downwards to unite with a median ventral bar (*v.r.*). The latter is expanded anteriorly to form a small flattened plate, which is perforated by a single small foramen. We were unable to find any trace in our specimen of the rostral appendages ('Anhang der Rostrum') figured by Gegenbaur (5).

At the anterior end of the cranium is a large fontanelle (*a.f.*) extending from between the two dorsal bars of the rostrum to the ventral bar of the rostrum. This fontanelle, which therefore occupies the whole of the anterior end of the cranium, is completely covered by a strong sheet of fibrous connective tissue.

When seen from the dorsal surface (text-fig. 2) the most prominent features of the skull are the large, lateral, wing-like expansions of the olfactory regions (*o.c.*). These expansions are dorso-ventrally compressed, and their distal extremities taper almost to a point. The orbits (*o.*) are situated immediately posterior to the distal portion of the capsules.

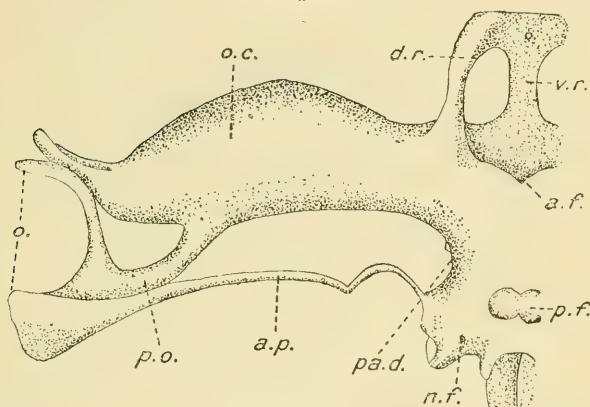
The depression into which the 2nd to 7th cranial nerves emerge in a normal skull also bears the eye, and is therefore the orbit. In *Zygæna malleus* the orbit is a separate structure, and we have therefore decided to call the depression into which the above mentioned cranial nerves emerge the *pre-auditory depression* (*p.a.d.*). This has resulted in a few other changes in the nomenclature of related parts, but it appears preferable to us to do this rather than to retain terms which give incorrect impressions of the relationships of the regions to one another.

The *orbit* is composed of a *post-olfactory process* (*p.o.*) which runs backwards and outwards from the olfactory capsule to form the anterior three-quarters of the circumference of the orbit on the dorsal surface. The orbit is completed dorsally by a bar of

cartilage, the *auditory process* (*a.p.*), which arises from the antero-dorsal corner of the auditory capsule. The auditory process broadens out distally, and the broad distal portion forms the posterior fourth of the orbit. The process throughout its length acts as a support to the posterior border of the hammer. The relations of this bar and the shape of the orbit are incorrectly figured by Gegenbaur (5).

The *olfactory capsules* are dorso-ventrally flattened and project laterally from the front of the cranium. They do not come into apposition with one another in the median longitudinal line. Each cartilaginous capsule is completely closed except for the small nostril, which is situated antero-ventrally and a short distance from the distal end.

Text-figure 2.



Dorsal View of Skull.

*a.f.* anterior fontanelle.  
*a.p.* auditory process.  
*d.r.* dorsal bars of rostrum.  
*n.f.* nerve foramen.  
*o.* orbit.

*o.c.* olfactory capsule.  
*p.a.d.* pre-auditory depression.  
*p.f.* posterior fontanelle.  
*p.o.* post-olfactory process.  
*v.r.* ventral bar of rostrum.

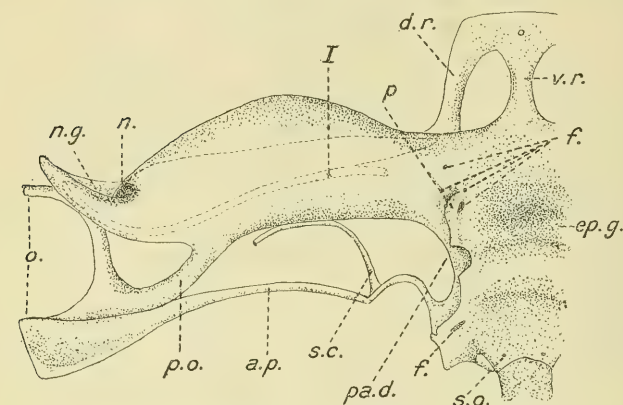
The cranium is slightly dome-shaped dorsally, and the auditory capsules are attached to it postero-laterally. Between the two auditory capsules, and on the dorsal surface of the cranium is a shallow median depression, the *posterior fontanelle* (*p.f.*). This fontanelle contains four apertures, two on each side, which will be referred to later in the description of the membranous labyrinth.

Each auditory capsule exhibits on its dorsal surface a *supra-auditory process* (*sa.p.*) which extends upwards from the socket, which is found on the side of the capsule, for the articulation of the hyomandibular. About half an inch mesial to each supra-auditory process is a small foramen for the passage of a nerve.

The ventral view of the skull shows that a groove, about one inch in length, runs from the distal end of the olfactory capsule to the nostril. The end of the capsule also serves as a further support to the anterior of the orbit. Gegenbaur (5) has incorrectly figured the extent of the cavity of the olfactory capsule and the position of the nostril.

A very slender bar (*s.c.*) of fibrous tissue, which is perforated by a fine canal, runs from the auditory process to the olfactory capsule, and then runs along the posterior edge of the capsule. The structure of this bar suggests that it is a sensory canal. It is figured as far as it could be traced in our specimen, but we do not believe that it is complete. It has been figured, for about a

Text-figure 3.



Ventral View of Skull.

*ep.g.* ethmo-palatine groove.  
*f.* foramina.  
*n.* nostril.  
*n.g.* nasal groove.  
*s.c.* sensory canal.  
*s.o.* 1st spino-occipital foramen.

*p.* process on cranium for articulation of ethmopalatine process.  
*I.* olfactory nerve. The dotted area anterior to the nerve indicates the extent of the olfactory sac.

third of the length shown in our drawing, by Gegenbaur (5), and he has lettered it (*x*), but does not explain it in any way.

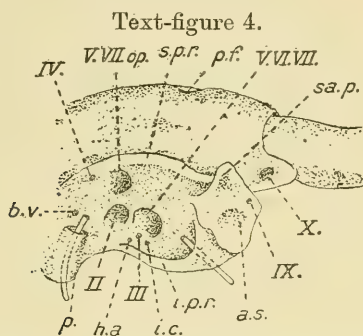
The ventral side of the cranium (text-fig. 3) is marked by a deep *ethmopalatine groove* (*ep.g.*) into which fits the narrowed middle portion of the upper jaw. On each side of this narrowed portion of the jaw is an *ethmopalatine process*. Each of these fits against a corresponding process (*p.*) on the cranium, one being situated immediately anterior to each of the two outer edges of the *ethmopalatine groove*. The processes on the cranium are perforated on the mesial side by a single large foramen, which opens dorsally into the pre-auditory depression. In addition in this region there are four smaller foramina on each side.

Another pair of large foramina, one on each side, is seen perforating the *inferior pre-auditory ridge* (*i.p.r.*), which runs anteriorly from the auditory capsule.

Two small apertures (*s.o.*) ventral to the foramen magnum serve for the passage of the first spino-occipital nerve.

The posterior view of the skull shows the apertures for the ninth and tenth cranial nerves in the normal position; the fairly large foramen of the vagus nerve (*x*) at the sides of the occipital processes, and the small foramen for the glossopharyngeal nerve (*ix*) at the postero-lateral corner of the auditory capsule.

The posterior portion of the skull seen in lateral view (text-figure 4) shows a number of foramina. The most posterior of these is that of the vagus nerve (*x*), and slightly anterior to this is the foramen of the glossopharyngeal nerve (*ix*).



Lateral View of Posterior portion of Cranium.

*a.s.* articular facet for hyomandibular cartilage.  
*b.v.* passage for blood-vessel.  
*h.a.* passage for hyoidean artery.  
*i.c.* interorbital canal.  
*i.p.r.* inferior pre-auditory ridge.

*p.* articulating process on ventral side of cranium. Seeker inserted to show large foramen.  
*sa.p.* supra-auditory process.  
*s.p.r.* superior pre-auditory ridge.  
 The posterior seeker marks the foramen perforating the inferior pre-auditory ridge.  
 II-X. Cranial nerves.

The pre-auditory depression exhibits the following apertures:—the largest, which is situated near the posterior of the depression, is the foramen of the fifth, sixth, and seventh cranial nerves (*v*, *vi*, *vii*), excepting the ophthalmic branches of the fifth and seventh nerves. Ventral to this are three small apertures, the anterior of which serves for the passage of the hyoidean artery (*h.a.*). The posterior of the three is the interorbital canal (*i.c.*). The third aperture, which is situated between and slightly dorsal to the others, is the foramen of the third cranial nerve (*iii*).

The large optic foramen (*ii*) is situated immediately anterior to the foramen of the chief branches of the fifth and seventh and



the sixth nerves, and the single foramen of the ophthalmic branches of the fifth and seventh nerves (v & VII, *op.*) is immediately dorsal to it.

In front of the ophthalmic foramen is a small aperture which serves for the exit of the pathetic nerve (IV), and ventral and slightly anterior to this is a small opening for the passage of a blood-vessel (*b.v.*).

The pre-auditory depression is bounded on its dorsal and ventral edges by well-marked *superior and inferior pre-auditory ridges*. The inferior ridge (*i.p.r.*) is the better developed and runs forward from the auditory capsule to the olfactory capsule. The superior ridge (*s.p.r.*) becomes less marked anteriorly and disappears before reaching the olfactory capsule.

#### MEMBRANOUS LABYRINTH.

As has been stated above, the posterior fontanelle of the cranium contains four apertures, two on each side of the median longitudinal line. The anterior and smaller member of each pair serves to transmit the *ductus endolymphaticus*, whilst the larger posterior aperture leads into the perilymph cavity surrounding the posterior vertical canal. The posterior aperture apparently corresponds to the tympanic aperture described by Howes (11) in *Raia*, and also mentioned by Goodey (6) as occurring in *Chlamydoselachus anguineus*.

Unfortunately the superficial portion of the ductus endolymphaticus was destroyed during the preparation of the skull, and we are therefore unable to give any account of its course outside the cranium. Judging, however, from the shallowness of the posterior fontanelle, and the fact that the skin was closely attached to the cranium in this region, it most probably runs straight to the dorsal surface of the head.

The *membranous labyrinth* (text-figs. 5 & 6) of the right side of the head has been dissected out, by removing the surrounding cartilage, and serves as the basis of the following description.

In this account we have adopted the nomenclature used by Stewart (15) in preference to that used by Retzius (14).

The *ductus endolymphaticus* (*d.e.*) runs downwards and bifurcates at its lower end; a main branch going to the *sacculus* (*s.*) and a smaller branch opening into the *recessus utriculi* (*r.u.*). Our observations on this point do not agree with those of Ayers (1), who states:—"I have not seen the bifurcate endolymphatic duct, described by Hasse for the species which he studied, but the two endolymphatic tubes observed by E. H. Weber I have found beautifully developed in *Sphyrna zygaena*, and there is not the slightest doubt as to their occurrence."

We have been unable to trace Hasse's statement in his paper (8) or to ascertain what species he studied. There is, however, no doubt whatever that the endolymphatic duct does bifurcate at its lower end. The second duct present is not an endolymphatic



duct but leads into the posterior perilymph cavity. This observation agrees with that of Goodey (6) on the posterior duct in *Chlamydoselachus anguineus*.

The *Utriculus*, as in nearly all Elasmobranchs, is divided into two portions, anterior and posterior, which do not communicate directly with one another, but indirectly through the sacculus.

The anterior utricle (*u.a.*) is circular in transverse section and gives off the *anterior canal* (*c.a.*) at its dorsal end. The canal runs forward and slightly outward, and expands at its lower end into the *anterior ampulla* (*a.a.*). The anterior utricle and the anterior canal together form an oval.

The anterior utricle also gives off posteriorly, at about the middle of its length, the *external canal* (*c.e.*), which runs at first downward and outward, and secondly horizontally. At its anterior end it expands into the *external ampulla* (*a.e.*), which communicates again with the anterior utricle through a short canal running dorsal to the recessus utriculi, but having no direct connection with it.

On the ventral side of the anterior utricle is a sac, the *recessus utriculi* (*r.u.*), which is somewhat flattened from side to side, and almost triangular in lateral view. It communicates with the anterior utricle through a small aperture, whilst another small aperture, situated near the opening into the utricle, opens into the sacculus.

The *posterior utricle* (*u.p.*) is the portion of the labyrinth situated nearest to the median longitudinal line of the cranium. It has direct communication with the sacculus through a short duct, the *ductus utriculo saccularis posterior* (*d.u.s.p.*). The dorsal end of the posterior utricle gives off the *posterior canal* (*c.p.*), which runs downward and outward and after expanding into the *posterior ampulla* (*a.p.*) opens into the ventral end of the utricle.

The *sacculus* (*s.*) and *lagena* (*l.*) are laterally compressed; the latter being given off as a simple pouch at the infero-posterior end of the sacculus. The outer face of the sacculus and lagena is directed outward at an angle to the median plane.

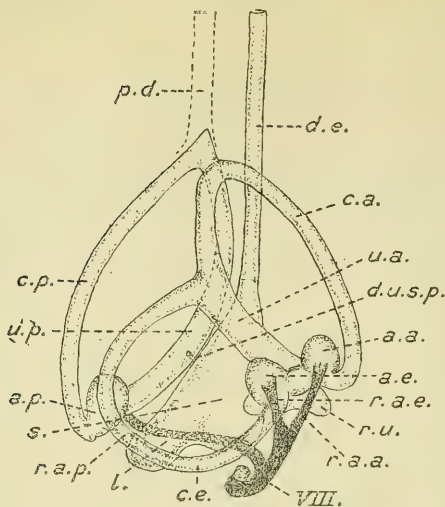
#### NERVE SUPPLY.

The membranous labyrinth is supplied by branches of the eighth cranial nerve.

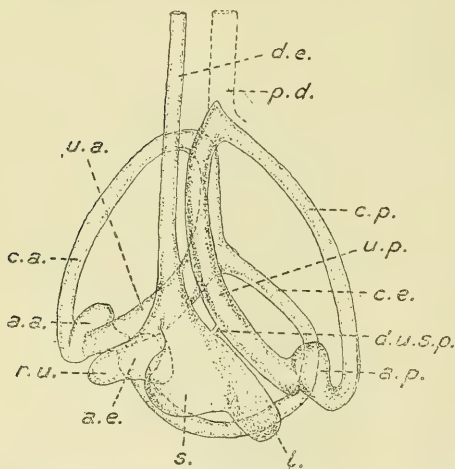
The main nerve gives off a branch which runs beneath the recessus utriculi and then bends upward. It then bifurcates to form the *ramulus ampulla anterior* (*r.a.a.*) and the *ramulus ampulla externus* (*r.a.e.*). A longer and finer branch, the *ramulus ampulla posterior* (*r.a.p.*), comes off from the main nerve and runs on the inner side of the sacculus to the posterior ampulla, giving off tiny ramuli to the sacculus and lagena *en route*. We were unable to trace the *ramulus utriculi* in our specimen, and it is probably very small.

The membranous labyrinth resembles in many respects that of *Cestracion philippi*.

## Text-figures 5 &amp; 6.



Right Membranous Labyrinth. (Outer view.)



Right Membranous Labyrinth. (Inner view.)

- |                                                     |                                          |
|-----------------------------------------------------|------------------------------------------|
| <i>a.a.</i> ampulla anterior.                       | <i>l.</i> lagena.                        |
| <i>a.e.</i> ampulla externus.                       | <i>p.d.</i> perilymph duct.              |
| <i>a.p.</i> ampulla posterior.                      | <i>r.a.a.</i> ramulus ampulla anterior.  |
| <i>c.a.</i> canalis anterior.                       | <i>r.a.e.</i> ramulus ampulla externus.  |
| <i>c.e.</i> canalis externus.                       | <i>r.a.p.</i> ramulus ampulla posterior. |
| <i>c.p.</i> canalis posterior.                      | <i>r.u.</i> recessus utriculi.           |
| <i>d.e.</i> ductus endolymphaticus.                 | <i>u.a.</i> utriculus anterior.          |
| <i>d.u.s.p.</i> ductus utriculo sacculus posterior. | <i>u.p.</i> utriculus posterior.         |
|                                                     | VIII. 8th cranial nerve.                 |

## BRAIN AND CRANIAL NERVES.

Busch (2) and Miklucho-Maclay (12) have briefly, and on the whole accurately, described and figured the macroscopic structure of the brain. Owing to the poor condition of our specimen we are not able to add much to their account, but there are a few points on which our observations do not agree with theirs.

The brain is antero-posteriorly shortened and, in dorsal view, only a portion of the *olfactory lobes* (o.l.), the *prosencephalon* (f.b.), the much convoluted *cerebellum* (c.), the *restiform bodies* (r.b.), and the short *medulla oblongata* (m.) are visible (text-fig. 7). The diencephalon and optic lobes are completely covered by the cerebellum.

The *prosencephalon* is single and shows no trace of a median fissure.

The large paired *olfactory lobes* are situated ventral to the prosencephalon; only their anterior ends being visible in dorsal view.

Owing to the intimate relation of the olfactory lobes and the prosencephalon Busch (2) has named them the "lobes communes," and a section through the forebrain appears to justify this name. On the other hand, in his diagram he shows the prosencephalon as a paired structure and the olfactory lobes as unpaired. This is opposed to our observations.

The *cerebellum* is roughly triangular in shape, the base of the triangle being closely apposed to the posterior of the prosencephalon, and its apex posterior. It is primarily divided into three segments; two of these being anterior, right and left, and the third running obliquely backward from the right. The left anterior segment is approximately equal in size to the posterior segment, but the right anterior segment is considerably smaller. All three segments are further divided into smaller segments, which in turn are sulcated.

Ventral to the posterior end of the cerebellum are two small oval lobes called by Miklucho-Maclay (12) the *lobi trigemini* (l.t.).

The *restiform bodies* (r.b.) are well developed and occupy their normal position. The *medulla oblongata* (m.) is very short, and the fourth ventricle is correspondingly reduced.

In ventral view the olfactory lobes completely cover the prosencephalon. The *optic chiasma* lies immediately posterior to the olfactory lobes.

The *infundibulum* is well developed, and the *sacculus vasculosus* shows on each side. Portions of the optic lobes are also visible in this view.

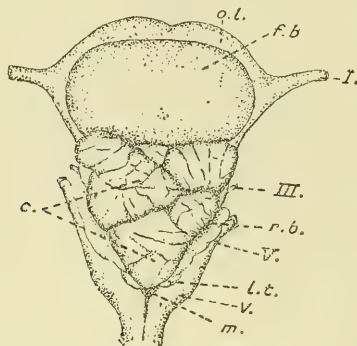
An examination of a median longitudinal section confirms Miklucho-Maclay's observation that a wedge-shaped portion of the cerebellum projects into the ventricle of the "Zwischenhirn."

The following Notes on the cranial nerves were made chiefly during the preparation of the skull, and are consequently far from complete.

The *olfactory nerve* is large and is given off laterally from the

olfactory lobe. It runs attached to the posterior border of the laterally elongated olfactory sac, which is placed in the laterally expanded olfactory capsule. The portion of the nerve adherent to the sac is called the olfactory bulb by Busch (2), whose figure shows it expanded rather more than is the case in our specimen. To verify Busch's statement we have sectioned a portion of the nerve taken from the region of the sac, but we have failed to find any trace of nerve cells. This, however, may be accounted for by the fact that our material was not in the best state of preservation.

Text-figure 7.



Dorsal View of Brain.

c. cerebellum.  
f.b. prosencephalon.  
l.t. lobi trigemini.  
m. medulla oblongata.

o.l. olfactory lobes.  
r.b. restiform bodies.  
v. 4th ventricle.  
I, III, V. cranial nerves.

The *optic nerve* runs on the ventral side of the hammer just anterior to the auditory process.

The *oculomotor nerve* runs for the greater portion of its length posterior to the optic, but crosses it ventrally about an inch from the orbit and is distributed to the inferior oblique, anterior rectus, and inferior rectus muscles. A distinct branch of the nerve runs parallel to the main branch and supplies the superior rectus muscle.

The *pathetic nerve* runs antero-dorsal to the optic and supplies the superior oblique muscle.

The *ophthalmic* branches of the fifth and seventh nerves run directly to the anterior end of the dorsal surface of the snout. The fifth, in addition, sends off a lateral branch to a patch of ampullary canals just mesial of the orbit.

The *mandibular* and *maxillary* branches of the *trigeminal* have the normal distribution.

The *abducens* runs ventral to the auditory process and supplies the posterior rectus muscle.

The *hyomandibular* branch of the seventh nerve runs posterior to the mandibular branch of the fifth and gives off an *external mandibular*.

The *auditory nerve* has already been described in relation to the membranous labyrinth.

#### SUMMARY.

The following are the important points dealt with in the paper :—

1. The skull, except the jaws, has been described in detail.
2. The membranous labyrinth has been described and figured for the first time.
3. The existing accounts of the macroscopic structure of the brain have been revised, and notes have been included on the relationships of most of the cranial nerves.

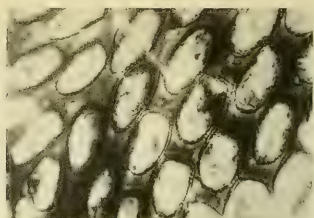
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- PROC. ZOOLOG. SOC.—1922, No. LXVI. 66





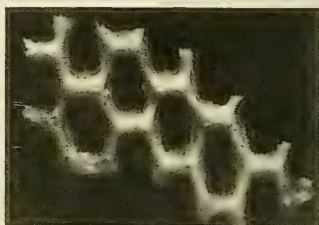




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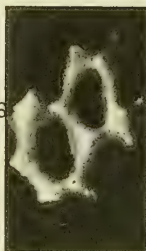
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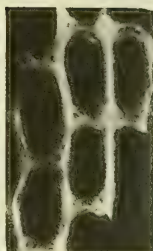
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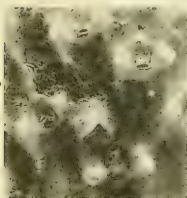
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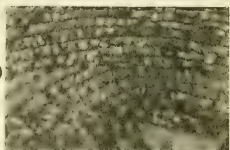
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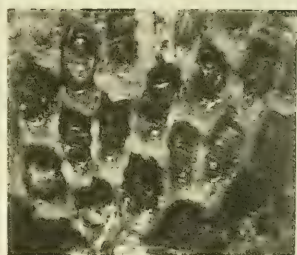
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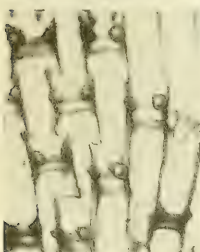
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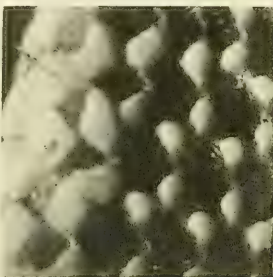
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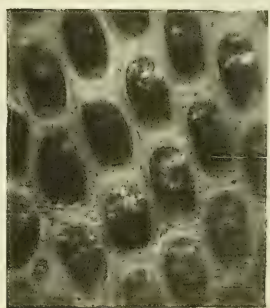
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II.



10







46. On an Instance of Commensalism between a Hermit Crab and a Polyzoon. By R. KIRKPATRICK, F.Z.S., and Dr. J. METZELAAR.

[Received August 4, 1922 : Read October 24, 1922.]

(Plates I., II.)\*

*General.*—In the year 1906, Mr. F. P. Vermeulen, Ymuiden, Holland, started with a fishery expedition to the West African shores with the object of seeing if the “langusts” of Cape Blanco and its neighbourhood would be worth exploitation. The rich material collected by him was given to the Zoological Society, “Natura Artis Magistra,” at Amsterdam. It contains many Hermit Crabs, the commonest of which is *Petrochirus granulimanus* Miers.

The younger specimens of this Crustacean live in small shells of *Turritella brevisalis*, *Natica fulminea*, *Nassa miga*, *Terebra senegalensis*, *Aporrhais pes pelecani*, and *Dorsanum politum*. These samples come from Cape Blanco and the large Greyhound Bay (“Baie du Levrier”) close by, from depths not exceeding 20 metres. A few specimens were also met with on the Senegal coast.

Now, some of these “youngster” home-shells show a thin incrustation of a Polyzoon, a few layers thick near the orifice and only one or two layers over the rest of the surface (Pl. I. fig. 3).

If we compare the older young and adult pagurids with the former, we notice the said colony has increased very much, resulting in a heavy turnip- or potato-like spheroidal mass, about 6 cm. in diameter (fig. 1), completely involving the original contour of the shell. At one side there is a funnel, about 2 cm. wide externally and filled in by the heavy claw of the *Petrochirus*. A section (fig. 2) shows the gastropod shell covered entirely by a dense, stony crust of the Polyzoon in numerous layers, amounting to 56. The shell-substance does not appear to have been eaten away as in shells encrusted by *Lepralia edax*. The free margin of the orifice of the larger specimens is made up wholly of Polyzoan layers folded on themselves (fig. 2). On dissection, the calcareous Polyzoan mass appears to be homogeneous, excepting that a few barnacles have been overwhelmed and suffocated. The most sound colonies have a perfectly smooth surface of a deep violet-brown colour in spirit, and they form a typical feature of the fauna of the Cape Blanco coast. But for reasons not yet explained the colony may lose its power of resistance against destructive forces of the environment. Everyone knows the difference between “living” mollusc-shells, so eagerly wished for by conchologists, and the porous, brittle shells, the legal inhabitants of which have been replaced by boring

\* For explanation of the Plates, see p. 990.

animals. Exactly the same is the case with our Polyzoön. The simple colonies from one station have all changed into microcosms of sessile invertebrate life. Large specimens of *Lithodomus* easily lodge in the thick, limestone-like wall without touching their motor-pagurid. There are the big colonies of a compound ascidian (*Distomus* sp.), purple barnacles, bushy hydroids upon the Polyzoan wall (Pl. II., fig. 14). Although very interesting from an ecological point of view, we shall not describe these compound colonies as they do not show *constant* features, the original Paguro-Polyzoan association having lost its exclusive character. Meanwhile it illustrates the fact that mobility of substratum is favourable to diverse forms of sessile animal life.

By the way, we may notice one rather striking fact. Although the weight of its limestone house with weeded roof *must* become a nuisance to the Hermit, however powerful it may be, let us mention one point in favour of its security. In one of the hydroid tufts a spawning *Sepia* has glued several eggs. So this professional crab-eater remained unconscious of the close proximity of its prey, and the most critical sceptic must admit that this argument, taken from nature itself, is stronger than any aquarium experiment as to the efficiency of this pagurine mode of life.

As a counterpart to this, we may add that remains of *Eupagurus bernhardus* are often found in the stomachs of Cod from moderate depths in the North Sea.

*Description of the Polyzoön*, based upon  $4\frac{1}{2}$  adult and 3 young samples sent to the Natural History Museum, London.

A glance with a good lens at once shows the Polyzoön to be a member of the great Membraniporidan group. The surface of the zoarium is covered with a membrane, which can be peeled off. The zoecia are arranged in straight, longitudinal rows, the latter every now and then bifurcating. The zoecia are not abreast transversely, but in quincunx. A five of diamonds in cards, with the pips uniformly enlarged till they nearly meet, would illustrate the plan.

The zoecia (Pl. I. figs. 4, 5, 6) are oval, and on an average 0.6 mm. long and 0.3 mm. wide in the middle. The margins of the zoecia in well-preserved material are mapped out by dark brown membranous or chitinous lines. Busk calls attention to similar "brown lines" in his description of *Membranipora denticulata* Busk.

The calcareous margin is strongly granulated, and slopes inwards and downwards to a finely serrated edge bordering the oval opesia.

At the proximal or basal end of each zoecium and immediately below the opesia there are two triangular, flattened, hollow tubercles, separate in the young stage, but joined into a single rectangular block in older zoecia (figs. 4, 5, 6). The brown line separately surrounds each triangular tubercle and also each rectangular block.

The ectocyst in the surface layer of zoëcia is membranous. The operculum is 0.06 mm. long and 0.08 mm. wide, and with the rim thickened, especially laterally. In the older layers of zoëcia the opesia is filled in, not by membrane, but by a thick punctate, calcareous plate, convex on its lower surface, and further, the zoëcial walls become thickened, so that the zoarium becomes hard and stony. Rosette-plates multiporal; usually four in each lateral wall; two, occasionally several, in the distal wall.

There are no avicularia and no oëcia.

There need be no hesitation in assigning the Polyzoon to the genus *Conopeum* Gray\* (genotype: *lacroixii* Audouin†) as amended by Norman‡ and Canu & Bassler§.

But the determination of the species has been a more difficult problem. One high authority, to whom the material had been sent, identified the species as *Membranipora tehuelcha* d'Orbigny. We were at first inclined to regard the species as a variety of *Conopeum lacroixii* Audouin, but finally we have come to the conclusion that the species is new to science. We propose to call it *CONOPEUM COMMENSALIS*, sp. n.

The distinguishing characters of the new species are: the thick zoëcial walls, the thick calcareous opesial plate, and the dense stony multilaminar zoarium. Neither the well-known British *Con. lacroixii*, as described by Busk and Hincks, nor the Mediterranean form, as described and figured by Audouin and Savigny, have any of these characters. If in the British form of *C. lacroixii* occasionally one layer grows over another, there are no calcareous opesial in-fillings; and, moreover, "the triangular hollows on each side above the aperture" (Hincks, Brit. Mar. Pol. p. 130) have each an opening, covered by membrane, and do not fuse into a single rectangular block. This fusion does, however, take place occasionally in the typical form, figured in the 'Description de l'Égypte,' pl. x. fig. 9. The new species differs widely from *M. tehuelcha* d'Orbigny. We had the good fortune to find numerous specimens encrusting the alga *Macrocystis pyrifera* from the Straits of Magellan and from Valparaiso and the coasts of the Tehuelchan region (the T. being a great tribe of Patagonian Indians). The zoëcia (fig. 12) are very different in shape and character, being thin-walled, elongated, rectangular boxes with sharp edges; and the triangular knob and fused rectangular structures of *C. commensale* Kirkpatrick & Metzelaar are replaced by a pair of rather long, blunt calcareo-chitinous "spines." *M. tehuelcha*, in our opinion, is little

\* Gray, List of British Animals.—Part I. Radiated Animals, pp. 108, 146 (1848).

† It is held by several authorities that Audouin's "*Lacroixii*" is a synonym of *Millepora reticulatum* Linné.

‡ Norman, Nat. Hist. East Finmark. Ann. & Mag. Nat. Hist. (7) xi. p. 586 (1903).

§ Canu & Bassler, North American Early Tertiary Bryozoa. U.S. Nat. Mus. Bull. 106, text pp. 84, 86 (1920).

other than a South American representative of *Membranipora membranacea* L.

The study of the triangular objects in *C. lacroixii* Audouin and in the early stages of *C. commensale* Kirkpatrick & Metzelaar has, we think, thrown an interesting light on certain structures found in widely separate families and genera. The precise nature of the "triangular hollows"\* in *C. lacroixii* is not definitely known, but the view that they are diminutive zoëcia, aborted owing to exigencies of space, appears to us a reasonable one. Cramped zoëcia are often found among the rows and layers of ordinary zoëcia. The openings of the inter-zoëcial triangular hollows of *C. lacroixii* have granulated margins, precisely comparable with the edges of ordinary zoëcia, and under a high power the whole structure is fairly similar in aspect to an ordinary zoëcial box somewhat distorted.

In *C. commensale* the triangles have a calcareous roof, and are bounded each by a separate brown line. Where the triangles are fused into one rectangular block, there is only one line round the block. A fundamental and—with the exception of *Loxosoma*—universal character of the Polyzoa is that of budding so as to form colonies. Limitation of space must lead to a struggle among the buds, with partial or complete suppression of some.

It would appear that in *C. lacroixii* each zoëcium gives off three distal buds, the lateral ones being almost, but not wholly, suppressed.

A careful examination of many species of Cheilostomes has convinced us that the paired spaces, knobs, tubercles, and spines so commonly present are all comparable with the "triangular hollows" of *C. lacroixii*, and that they are modified zoëcial buds† taking on strange shapes and functions. In *Membranipora membranacea* L., for instance, triangular spaces will be found at or near the growing edges of the zoarium; in older cells the "hollows" (really inter-zoëcial boxes) grow up into long spines or tubercles, as if, owing to the limited basal area, they took to building skyscrapers.

In *M. tehuelcha* d'Orbigny (fig. 12) the same event has happened. Here the tops of the spines are often membranous, recalling the membranes over the openings of the triangles in *C. lacroixii*. That this interpretation is not a mere fancy, is shown by the resemblance of the early stages of the spines near the growing edges of colonies to the triangular areas in *C. lacroixii*.

In *M. tuberculata* Bosc, so abundant on Gulf weed, the

\* Hincks, 'British Marine Polyzoa,' p. 130.

† Cf. the "origellæ" of Jullien, "des bourgeons charnus, développés sur l'endocyste," which can reproduce zoëcia, avicularia, etc. (Bull. Soc. Zool. France, xi. p. 607, 1886). Later, "joncturées," which produce zoëcia, are distinguished from "origelles évolutives," which form avicularia, spines, etc. (Jullien & Calvet, Bryozoaires 'Hirondelle,' 1903, p. 18).



tubercles, at first separate, may join together to form single blocks as in *C. commensale*; a remarkable example of the former species is shown in fig. 11, where the blocks have developed so enormously as almost to obliterate the opesia.

In descriptions, the triangular hollows, spines, tubercles, etc. are usually associated with the distal or oral end of the zoecium, but they should perhaps rather be associated with the proximal or basal part of a zoecium. On the triple-bud hypothesis it is certainly more rational to associate the three buds, no matter what their subsequent history and disguise might be; and further, the knobs, spines, etc. are often clearly seated on the front of the basal end of a zoecium. Take, for example, the little knobs on the zoecia of *Membranipora savartii* Audouin, shown on the base of each cell in Savigny's figure ('Description de l'Egypte,' Atlas, pl. x. fig. 10) \*.

In *Thairopora armata* MacGillivray (fig. 13) the two club-shaped tubercles are situated one on each side of the oral orifice of a zoecium, and, it must be admitted, a little imagination is required to realize that even here the tubercles should perhaps be associated with the proximal end of the following zoecium. One might assume that the two lateral buds had been given off at right angles to the central one, instead of at a forward-opening acute angle.

The avicularian cell in this species appears beautifully to confirm the theory of homology of tubercles and triangular boxes; for here, in place of tubercles, and on each side of and above the avicularian opening, there is a triangular box with a clear space in the roof (fig. 13).

Possibly the quincuncial plan of growth so common in Cheilostome Polyzoa may be due to adaptation to limited space. Zoecia giving off three buds at the distal end would not be well able to grow abreast; accordingly the buds (and their adult equivalents) often alternate transversely.

The fusion of two lateral hollow knobs into one rectangular hollow box in *C. commensale* may be connected in some way with reproduction, for in decalcified specimens there can usually be seen a brown body or developing new polypide in the zoecial cavities adjacent to these boxes.

*Discussion.*—On two points our description of the new species is open to adverse criticism. Firstly, we attribute specific value to zoarial characters. During an early period of the study of Polyzoa, zoarial characters alone were considered, most of the encrusting and branching calcareous Cheilostomes being relegated to *Lepralia* and *Eschara* respectively. Later, zoecial characters became all-important, the zoarial ones being entirely put aside. At the present time the tendency is to take all characters into

\* There is rarely any trace of the knobs in the specimens of this species from tropical seas or from Japan.



consideration, judging each case on its own merits. A good example of the specific value of zoarial characters is afforded by *Lepralia bifurcata* Waters, found in deep-water off Capri. Here we have a typical *Lepralia*, but one that always grows in a very definite, peculiar, and characteristic way, viz. as a bifurcating colony with two little wings. No matter how closely the characters of the individual zoecia resemble those of some particular encrusting *Lepralia*, it would be difficult to regard the bifurcating colony as a mere variety or variation of the encrusting one. Similarly, we regard the dense, stony, multi-laminate Polyzoon from Cape Blanco as specifically distinct from the slender, thinly encrusting *C. lacroixii*, the modified character—if we may adopt the neo-Lamarckian line of thought—having perhaps resulted from epœcal, e. g. well-fed life.

*Biology.*—Again, the adoption of the name "*commensale*" might be considered a doubtful proceeding. We think the name, however, to be convenient, not only from the point of view of easy identification, but justifiable as indicating the real relationship existing between the Polyzoon and the Crustacean. There is evidently no question of true symbiosis or mutualism *sensu strictiore*, if we define that as "legal relation between two different organisms," principally, because *Petrochirus granulimanus* can live and thrive without *C. commensale*. Leaving the young Crustacea aside, we find the adults associated with the sponge *Suberites domuncula*, the compound zoantharian *Corticifera lutea*, and the Polyzoon *Lepralia edax*.

But the reverse does not seem to be the case. Polyzoa growing on the hydroids and corals of the Vermeulen-expedition did not include *C. commensale* among them. Nor did we notice it upon living molluscs from the same localities. Possibly the Polyzoon could survive for a time on an untenanted shell with much diminished vitality, but so far there is no evidence on this point, although we must take into consideration that the West African material has been collected by one who was not a zoologist.

According to Prof. Calvet, any smooth surface is suitable to the Membraniporæ, and "associations of hermit-crabs and Polyzoa are common enough." Even so, we never saw them before in such a definite non-accidental mode and shape. The Paguro-Polyzoan association described here appears to be a definite and not an accidental one; the Crustacean and Polyzoon being more to each other than casual messmates; for it is certain they derive special advantages from each other's presence.

Hermit Crabs are widely distributed all over the world, and are notorious for their militant and aggressive nature. Ensconced in their shells they are veritable tankers, spreading dismay among their helpless victims. Every now and again, when the soldier has to leave his fortress, his softened body is exposed to danger. But frequently some other organism (Sponge, Cœlentérate or, more rarely, Polyzoon) adapts itself to the shell, and gradually acquires certain special characters. The encrusting

animal forms an extra panoply, not merely thicker, but more extended, especially around the shell orifice, thereby generally ensuring a longer tenancy to the Crustacean. This feature of extended growth is illustrated in fig. 2, where the opening of the fortress is seen to be formed, not of shell, but of infolded layers of the Polyzoon. Again, the Polyzoon obviously benefits; for it is in alliance with a vigorous and successful marauder, and although sedentary by nature, is continually being carried to new and rich pastures.

Accordingly, the large size of the new species is not surprising.

We return now, after this economic excursion, to the peculiarity of the association described. Against critics who deny the non-accidental nature of it, we draw attention to one main point. Setting apart those favourite Pagurine mates: *Suberites* and the epœcal Zoantharians, there remains the fact that a "special seat" is reserved to *Conopeum commensale* among the hosts of sessile epœcal animals, ready to populate every available spot in the tepid tropical coast-waters. In a very short lapse of time a typical complex is formed. This follows from the fact that among the many home-shells of adult *Petr. granulimanus* only one was found naked, obviously inhabited only a short time before it was caught; intermediate gradations to full-grown adult colonies are wanting. Now, what is the reason that among so many rivals the tiny Polyzoon regularly wins the battle? We have seen that the other candidates may win the second round if the Hermit migrates to a spot unfit for its Polyzoon comrade to live in. In the struggle for life the champion is slain at last. Now at last a fair chance is given to everybody; here you have Accident playing its part, and the result . . . a chaotic conglomerate of sessile marine life (fig. 14).

Since the time of Darwin, Law has taken the place of Accident in biological science.

Our case is in some respects comparable to the well-known association of *Eupagurus bernhardus* and *Hydractinia echinata*. In this case the Pagurid inhabits the whole "littoral" region up to a depth of 270 metres, but *Hydractinia echinata* is a coastal form which does not follow the adolescent *Eupagurus* to depths exceeding those of the centre of the North Sea. At the lower limit of its occurrence the *Hydractinia* is often replaced by *Alcyonidium gelatinosum*. Now, although *Hydractinia echinata* has been found in a few instances without its mate *Eupagurus bernhardus*, is there anybody who will seriously contest the particular relation between these two organisms? Cf. *Eupag. pubescens*, which occur in the North Sea as a rule, associated with *Suberites ficus*, but exceptionally with *Zoanthus* sp.

So far as we know, the present case has not yet been described. It is a remarkable fact that Chevreux and Bouvier, among the rich material of the 'Melita,' described 17 species of Pagurids (Mém. Soc. Zool. France, v. 1892), but only noticed "coquille

recouverte de bryozoaires" in the case of *Petrochirus granulimanus*. The "bryozoaires" have probably been *Con. commensale*, but they were not examined.

In the volume dealing with the results of the inquiries of the 'Travailleur' and 'Talisman' immense numbers of Polyzoa are mentioned, but no reference to the present case.

*Summary and Conclusion.*—The present Polyzoon from the Cape Blanco region is a new species, viz. *Conopeum commensale* Kirkpatrick & Metzelaar. It is most nearly related to *C. lacroixii* Audouin.

The paired "triangular spaces," paired knobs, tubercles, or spines so commonly present in many species of Cheilostome Polyzoa are probably aborted zoecial buds, more or less suppressed or modified owing to lack of space for free growth.

The association with the Crustacean *Petrochirus granulimanus* is a definite, not an accidental one, being a case of commensalism in the sense of Van Beneden.

#### EXPLANATION OF THE PLATES.

(The figures to be examined through a hand-lens.)

##### PLATE I.

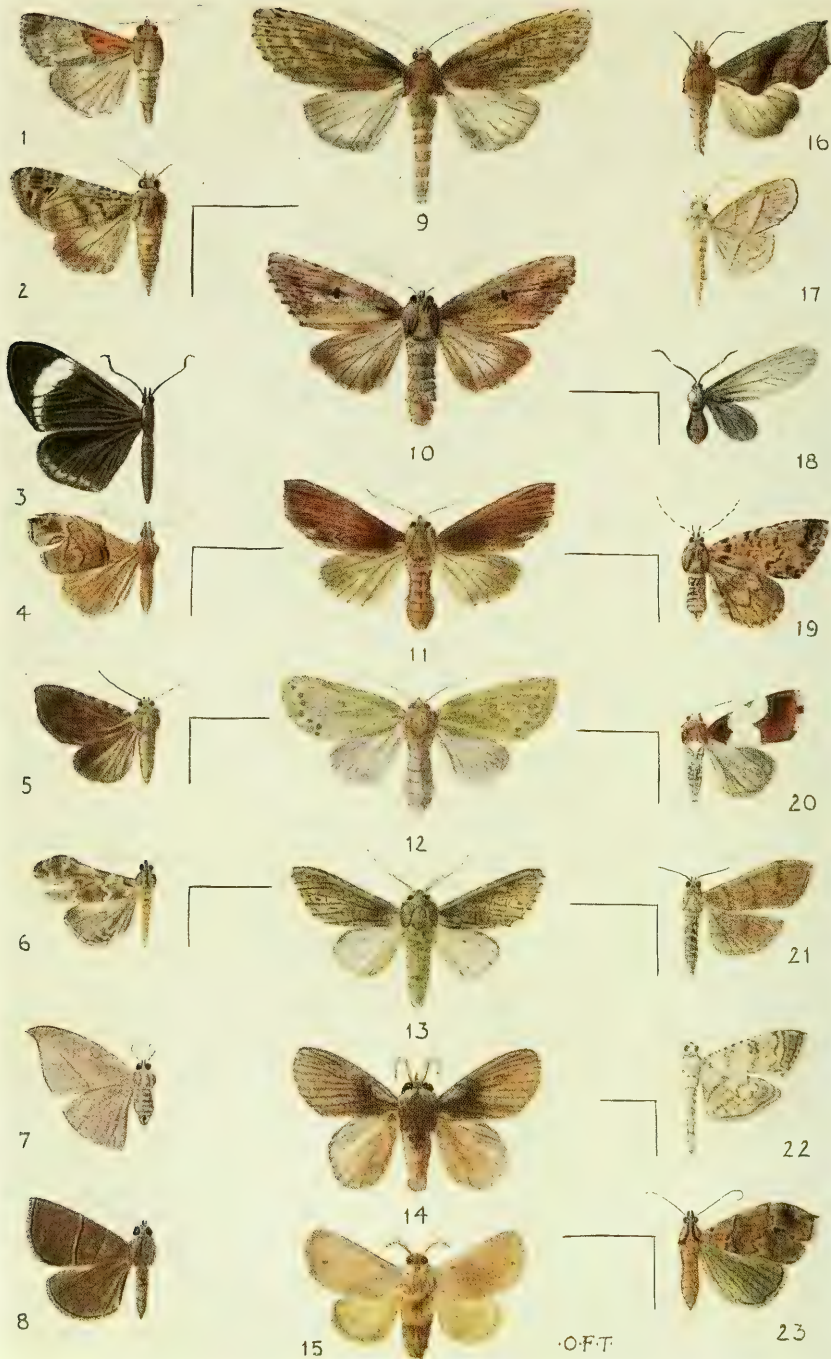
- Fig. 1. Gasteropod shell inhabited by *Petrochirus granulimanus* Miers, completely encrusted by the Polyzoon *Conopeum commensale* Kirkpatrick & Metzelaar from Cape Blanco. Nat. size.
2. A shell and Polyzoon crust cut in half. Nat. size.
3. *Turritella* shells inhabited by Hermit Crab, and each encrusted by young colony of *Conopeum commensale*: from Senegal. Nat. size.
4. *Conopeum commensale*.  $\times 20$ .
- 5 & 6. The same from another specimen, showing at the first separate triangular tubercles and the single rectangular blocks.  $\times 20$ .
7. An older layer of zoecia broken into and viewed from the inferior or dorsal aspect, showing calcareous infillings of the opesiæ.  $\times 20$ .
8. *Conopeum lacroixii*, showing the two separate triangular "spaces" (boxes) at the base of each zoecium.  $\times 20$ .
9. *Conopeum commensale*. Transparent vertical section, showing layers.  $\times 3\frac{1}{2}$ . (Cf. fig. 2.)
10. *Conopeum lacroixii* Audouin, showing separate triangular hollows: specimen from Dovercourt, England.  $\times 20$ .
11. *Membranipora tuberculata* Bosc, encrusting two sides of alga from Algoa Bay; showing remarkable blocks at the margin of colony, also ordinary paired tubercles.  $\times 20$ .
12. *Membranipora tehuelcha* d'Orbigny on *Macrocytis pyrifera* from South America; showing the two spine-like tubercles to each zoecium.
13. *Thairopora armata* MacGillivray, showing zoecia with paired boss-like tubercles and an avicularian cell with triangular hollow boxes above mandible.  $\times 20$ .

N.B.—There is an avicularium with sharply-defined triangular mandible about 8 mm. above the middle of the lower border of the picture. The mandible and the triangular boxes above it have a frog's-face-like aspect. In the ordinary zoecia the pairs of white boss-like tubercles replace the triangular "hollows" or boxes. A lens is necessary.

##### PLATE II.

- Fig. 14. Bulbous specimen secondarily overgrown with hydroid, etc.





NEW SPECIES OF TRINIDAD MOTHS



## 47. New Species of Trinidad Moths. By W. J. KAYE, F.E.S. \*

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(Plate I.†)

The moths here described and figured were all (except one, *Centronia plorator*, caught by myself) taken by Sir Norman Lamont in the south of the island of Trinidad. Most likely, all the species will some day also be found on the mainland in either Venezuela or Guiana, as, except for numerous local races, one would not expect distinct island species such as are found in Oceanic islands, Trinidad being essentially a recently detached portion of Venezuela. Doubtless, there are numbers of species still unknown and undescribed, and very much work remains to be done before we can even approximately guess the number of genera and species that exist.

## Family HYPSIDÆ.

*CENTRONIA PLORATOR*, sp. n. (Pl. I. fig. 3.)

♀. Base of eyes and base of palpi orange. Antennæ filiform. Abdomen black with the segments below ringed with white. Fore wing black with a postmedian curved white band commencing very narrow on the costa but rapidly widening to about 3 mm. wide as far as vein 4, where it rapidly contracts and becomes suffused with black to extreme angle of wings. Veins showing grey on inner side of white band. Hind wing dark bluish black with a narrow whitish marginal band, suffused with black as far as vein 5, where it suddenly ceases. Below, the white band of both fore and hind wing completely white without any suffusion. Exp. 44 mm.

*Habitat.* Trinidad, Siparia, 18. xi. 20 (*W. J. Kaye*). In Coll. B.M.

## Family NOTODONTIDÆ.

*DICENTRIA NONDESCRIPTA*, sp. n. (Pl. I. fig. 9.)

Head brown with a fan-shaped tuft of raised hair behind antennæ. Fore wing dark chocolate-brown with greenish-yellow shades, especially on costa beyond middle. Discoidal spot not conspicuous, of the same ground-colour as wing and edged on both inner and outer edges with greenish yellow. An indistinct slender pale line consisting of lunules beyond middle. Subterminal line also of pale lunules. A very ill-defined double submedian line, becoming lost in the ground-colour soon after leaving the cell. Hind wing pearly transparent with the apex

\* Communicated by GUY A. K. MARSHALL, C.M.G., D.Sc., F.Z.S.

† For explanation of the Plate, see p. 998.

darker. Inner margin also dark and a pale but distinct mark just below anal angle. Fore wing below shining blackish. Hind wing below shining whitish with a small dark mark in the middle of costa. Exp. 54 mm.

*Habitat.* Trinidad, Palmiste, 25. xii. 20 (*N. Lamont*).

*BORIZA KALODONTA*, sp. n. (Pl. I. fig. 13.)

Fore wing greenish grey mixed with slaty purplish. A conspicuous, elliptical, pale tawny spot between veins 2 and 4 near margin. Basal area to end or beyond cell slaty grey with three parallel wavy lines. A short, slender, black dash. Inner margin pale greenish. Outer margin broadly paler than rest of wing, with the veins showing through conspicuously. A small black dot between veins 3, 4, and another between veins 6, 7. Hind wing white with the costa narrowly dark brown, divided at middle with white. Thorax olive-brown. Fore wing below white with the veins 5, 6, and 7 heavily smoky. Costa immediately above pale tawny. Hind wing below pure white. Exp. 40 mm.

*Habitat.* Trinidad, Palmiste, 30. x. 11 (*N. Lamont*).

*PHASTIA MARICOLOR*, sp. n. (Pl. I. fig. 12.)

Fore wing pale sea-green. Discoidal spot purplish white. Subterminal series of large irregular spots, purple on the inside and white exteriorly. A short purplish basal streak. Beyond this is a faint ill-defined band, becoming very broad on inner margin, of a darker shade of green to the ground-colour. Beyond discoidal spot is also a poorly-defined narrow band. Thorax of same ground-colour as fore wing. Hind wing very pale grey, darker towards the outer margin. Under surface of both fore and hind wing yellowish white, the whole of the fore wing except the narrow inner margin dusted with blackish. Fore legs with the first joint of the tarsus clothed with yellowish-green hair. Exp. 42 mm.

*Habitat.* Trinidad (*N. Lamont*).

*RIFARGIA BRÜNNIPENNIS*. (Pl. I. fig. 11.)

Fore wing dark burnt-umber with a purplish shade. with the basal half the darkest. A short dark basal streak. Costa near apex and inner margin except at base tawny. A conspicuous, little, white, wedge-shaped mark between veins 2, 3 close to margin. Veins 4, 5, and 6 edged with tawny. Hind wing brownish grey, darker towards outer margin and darkest at anal angle. A very inconspicuous postdiscal line, becoming duplicated on vein 3 to inner margin. Fore wing below dull blackish. Hind wing below as above. Cilia black at termination of veins. Thorax tawny. Abdomen rather darker. Exp. 46 mm.

*Habitat.* Trinidad, Palmiste, 25. xii. 20 (*N. Lamont*).

## Family NOCTUIDÆ.

## Subfamily ERASTRIANÆ.

## BRYOLIMNIA MONODONTA, sp. n. (Pl. I. fig. 20.)

Third joint of palpi, frons, and base of antennæ white. Thorax light brown with a pair of white tufts behind. Fore wing with the base chocolate-coloured, followed by a broad pure white band deeply toothed on outer edge and with a small chocolate spot on costa. Postdiscal area chocolate, lighter towards inner margin and darkening towards costa. Cilia white, with a square dark spot about middle and with the tornus chocolate. Hind wing smoky greyish black, the apical area much the darkest. Discoidal spot indistinct, blackish. Abdomen greyish black. Exp. 26 mm.

*Habitat.* Trinidad, Siparia, 16. vi. 18 (*N. Lamont*).

## BRYOCODIA CRYPTOGRAMMA, sp. n. (Pl. I. fig. 19.)

Palpi with the first joint brown, the second and third whitish with dark brown marks. Fore wing dull olive greenish with pink and brown markings. A dark mark at base and a heavy brown basal line. A median fascia most prominent at costa and much broken at and beyond middle. A postmedian, thin, much-curved line, most prominent on veins 1, 2 and 4, 5. A dark curved apical fascia and a dark brown spot at tornus. Hind wing coloured as fore wing, with double submedian brown lines and a deeply curved postmedian single line. Underside of fore wing below cream-coloured with dark median and postmedian lines; a broad outer marginal fascia dark brown. Hind wing below coloured as fore wing, except that in the region of the anal angle the dark brown fascia is broken up with the pale ground-colour. Exp. 28 mm.

*Habitat.* Trinidad: Caparo, Oct. 1904 (*Birch*); Palmiste, 27. xi. 15 (*N. Lamont*).

## PARANGITIA NIGROFULGENS, sp. n. (Pl. I. fig. 5.)

Palpi, collar, and patagia yellowish brown. Abdomen fawn-coloured. Fore wing dark shining coppery black. A double indistinct waved black line close to base. Apex lighter than rest of wing and followed by indistinct double black lines. A curiously placed black angular mark on vein 2 close to edge of cell. Hind wing black with the whole of the large inner area dark cupreous grey. Fore wing below dull black with the inner marginal area paler. Underside of hind wing rather dark slaty grey with a darker marginal band. Exp. 24 mm.

*Habitat.* Trinidad (*N. Lamont*).

## PARANGITIA MICAPENNIS, sp. n. (Pl. I. fig. 2.)

Fore wing shining brownish olive. A large apical area, extending along costa to above end of cell and to tornus, paler with several short dark dashes. Discal spot uniform pale with a short black dash at its lower extremity externally. Opposite and close to outer margin a small black spot. Above these marks in certain lights are to be seen three short, parallel, brown dashes. Two short wavy lines above one another emanating from the outer margin. Hind wing blackish brown with a broad dark marginal band and a small yellow elongated mark at anal angle. Thorax with long raised scales. Abdomen with a raised tuft on third segment. Exp. 30 mm.

*Habitat.* Trinidad (*N. Lamont*).

## Subfamily NOCTUINÆ.

## SANYS IMPLACATA, sp. n. (Pl. I. fig. 17.)

Head, thorax, and abdomen pale brownish white. Fore wing narrow with the apex and inner margin rounded, pale brownish, darkest on the costa. A small blackish dot at origin of vein 2. A straight brown line across basal area and a slightly oblique postmedian line. A wavy double submarginal line greatly angled near tornus and a series of dark dots on margin. Hind wing similarly coloured to fore wing. A well-marked straight line across centre of wing, stopping at vein 6. A wavy, partly double, subterminal line much broken from vein 5 to apex. Exp. 30 mm.

*Habitat.* Trinidad (*N. Lamont*).

## PLUSIODONTA CUPRISTRIA, sp. n. (Pl. I. fig. 16.)

Fore wing dark purplish. A large burnished-copper patch at tornus and a central stria of same colour from the cell to the "tooth" of the inner margin. A pale oblique streak from apex to vein 2. At apex the streak is reflexed to costa. Thorax purplish. Two short subcostal streaks before apical streak. A small shade of copper-colour in middle of outer margin. Hind wing white with a broad dark margin, shading off internally with the white ground-colour. Underside of fore wing dark brown with the costa narrowly pinkish ochreous. Hind wing below white with only a small dark area at apex. Exp. 40 mm.

*Habitat.* Trinidad, Palmiste, 8. i. 21 (*N. Lamont*).

## Subfamily DELTOIDINÆ.

## EPTOMIPTERA PURPURASCENS, sp. n. (Pl. I. figs. 4, 23.)

Fore wing purplish with a broad, somewhat darker, central fascia, greenish on inner side from inner margin for half the length of wing. A slender wavy pencil-line within the fascia a little beyond middle. Outer edge of fascia very sinuous and



a slight greenish flush near tornus. Extreme apex with a short dark mark followed by a dark greenish-purple patch. Close to base a small dark dot. Hind wing purplish brown with a central dot followed by a dark indistinct line. Hind wing beneath much paler, and, in addition to the dot and dark line, there is a broad marginal fascia enclosing a pale wing-line. Exp. 28 mm.

*Habitat.* Trinidad.

EPITOMIPTERA MARMORATA, sp. n. (Pl. I. fig. 6.)

Fore wing various shades of pale brown with white lines. Extreme base pale followed by light brown fascia edged exteriorly with a sharply-defined white line sharply angled near inner margin. Central broad fascia darker than basal band, but also edged with a white line which is broken and very incomplete in central area but well-defined near costa and inner margin. Apex much mottled with white and brown followed by a wavy short white line. Hind wing pale light brown with a dark central oblique shade, followed by a short much-angled white mark, followed again by a slender white wavy line. Exp. 25 mm.

*Habitat.* Trinidad, Guaico, 18. iv. 15 (*N. Lamont*).

HYPENA BRODESCENS, sp. n. (Pl. I. fig. 8.)

Head, thorax, patagia, and metathorax very dark brown. Abdomen blackish brown with darker dorsal tufts of hair on the first four segments. Fore wing olivaceous dark brown with an oblique basal whitish line; a median broader straight white line. A postmedian series of yellowish spots on the veins and a very fine subterminal pale dotted line. Hind wing dull blackish with a pale bluish submarginal line most distinct between veins 1 and 3. Exp. 36 mm.

*Habitat.* Trinidad: Caparo, Nov. 1904 (*F. Birch*); Palmiste, 14. v. 21 (*N. Lamont*) (type), 20. xii. 21 (*N. Lamont*).

Family LIMACODIDÆ.

SISYROSEA GUAICA, sp. n. (Pl. I. fig. 15.)

Head and collar light brick-red. Thorax fawn-coloured; abdomen fawn-coloured with a reddish dorsal shade. Fore wing pale pinkish buff. A small black spot at the base of the cell and another black spot close to outer margin lying on vein 4. Cilia shining buff-colour. Hind wing buff, the cilia of the same colour. Underside of fore wing buff, with some darker shading towards costa. Underside of hind wing buff. Exp. 34 mm.

*Habitat.* Trinidad, Guaico, 18. ix. 15 (*N. Lamont*).

Family LASIOCAMPIDÆ.

HYDRIAS ALBIOCHREA, sp. n. (Pl. I. fig. 14.)

Head and thorax grey with some ochreous hairs. Fore wing



rather pale brown with scattered grey scaling. At base a short black streak above which is an irregularly-shaped greyish patch. This on costa is followed by two short curved lines. Some very indistinct, slender, wavy lines across the discal area, with the veins showing darker. Hind wing with the costal third greyish white with two or three indications of transverse lines. Basal two-thirds of wing tawny, pale at outer margin. Abdomen tawny, with some black scaling on the three basal segments. Exp. 42 mm.

*Habitat.* Trinidad, Port of Spain, 27.i.21 (*N. Lamont*).

#### Family URANIADÆ.

SYNGRIA DELICATA, sp. n. (Pl. I. fig. 7.)

Collar whitish. Thorax and abdomen pinkish fawn-colour, irrorated with minute black dots. Fore wing pinkish fawn-colour. Discoidal spot small, black, lunar-shaped, externally edged with pale cream-colour. A submedian, very indistinct, orange line running very obliquely. A very distinct postmedian ochreous line, palish-edged internally, also very oblique and sharply angled just below vein 6. Margin sharply defined ochreous, edged with pale colour internally. Hind wing pinkish fawn with fine irroration of black dots. Very indistinct sub- and post-median ochreous lines. Margins as in fore wing. Fore and hind wing below without markings, except the fine black dusting, which is less than on upper side. Exp. 36 mm.

*Habitat.* Trinidad, Palmiste, June 1915 (*N. Lamont*).

#### Family PYRALIDÆ.

Subfamily POCOCERINÆ (= *Epipaschianæ*).

POCOCERÀ BRUNNAPEX, sp. n. (Pl. I. fig. 1.)

Head and thorax reddish brown. Abdomen pale brown. Fore wing with basal third pinkish brown with some short darker longitudinal lines terminated by a somewhat sinuous silvery-grey line. Discal area of wing silvery grey, containing a much waved slender line in middle. A darker shade before outer margin and a dark reddish-brown apex with the veins showing through, heavily scaled with blackish brown. Hind wing pearly transparent with the apex blackish. Fore wing below with a dark red costa, and the remainder of the wing blackish. Hind wing below also with costa dark red, but otherwise as above. Exp. 38 mm.

*Habitat.* Trinidad, Guaico, 18. ix. 15 (*N. Lamont*).

Subfamily AGROTERINÆ (= *Pyraustinae*).

SAMEA DELICATA, sp. n. (Pl. I. fig. 22.)

Head pale straw-coloured. Patagia with dark brown spots on

frontal edge. Fore wing pale straw-coloured with two dark spots on costa close to base and some further minute points as far as end of cell. A submedian, a median, and a postmedian slender line. Beyond the last is a dark marginal band. Discoidal spot formed of a double ring, the one above the other. Hind wing pale straw-colour with three transverse lines, the inner one straight but oblique. The middle line greatly angulated in middle, and the last line greatly angulated beyond middle. A very fine dark subterminal line. Exp. 16 mm.

*Habitat.* Trinidad (*N. Lamont*).

*PHOSTRIA DUPLICATA*, sp. n. (Pl. I, fig. 21.)

Head and thorax dull ochreous brown. Fore wing ochreous brown. Basal line curved dark brown. Discoidal spot linear dark brown. Postmedian line heavy dark brown, greatly set-back between veins 2 and 3. Fine dark points at extremities of veins, and colour of wing beyond postmedian line darker somewhat than remainder. Hind wing darker than fore wing and blacker. A small dark spot within the cell and a curved median dark line, broken and waved between veins 2 and 3. Abdomen with the segments edged with white. Fore wing below buff with black discoidal spot and dotted postmedian line. Hind wing below buff with point in cell and faint indication of median line. Exp. 26 mm.

*Habitat.* Trinidad (*N. Lamont*).

Family ZYGÆNIDÆ.

Genus LAMONTIA.

Head small; antennæ long, slender, bipectinated. Abdomen small and rather slender. Fore wing long and narrow; veins 4, 5 very close together at origin; veins 8 and 9 stalked with 10, vein 11 weak, 12 strong. Hind wing with veins 4, 5 from same origin; vein 7 from a long way from 6. Outer margin of wing rounded. Vein 8 approaching very close to 7 and connected with the usual short bar.

*LAMONTIA CALIBANA*, sp. n. (Pl. I, fig. 18.)

Head, coxæ, pectus, and abdomen metallic greenish. Antennæ black, bipectinated to the tip. Collar and patagia with some pale mauve scales. Fore wing long and narrow, black at base and along the veins and costa, gradually becoming transparent (fugitive scaling) outwardly. Hind wing black, completely scaled, short, and much rounded. Exp. 30 mm.

*Habitat.* Trinidad, Rock, 1. i. 18 (*N. Lamont*). In Coll. Lamont.

## EXPLANATION OF THE PLATE.

- |                                               |               |
|-----------------------------------------------|---------------|
| Fig. 1. <i>Pococera brunnapex</i> , sp. n.    | Pyrilidæ.     |
| 2. <i>Parangitia micapennis</i> , sp. n.      | Noctuidæ.     |
| 3. <i>Centronia plorator</i> , sp. n.         | Hypsidæ.      |
| 4. <i>Epitomiptera purpurascens</i> , var.    | Noctuidæ.     |
| 5. <i>Parangitia nigrofulgens</i> , sp. n.    | Noctuidæ.     |
| 6. <i>Epitomiptera marmorata</i> , sp. n.     | Noctuidæ.     |
| 7. <i>Syngria delicata</i> , sp. n.           | Uraniadæ.     |
| 8. <i>Hypena brodescens</i> , sp. n.          | Noctuidæ.     |
| 9. <i>Dicentria nondescripta</i> , sp. n.     | Notodontidæ.  |
| 10. <i>Dicentria klagesi</i> Druce.           | Notodontidæ.  |
| 11. <i>Rifargia brunnipennis</i> , sp. n.     | Notodontidæ.  |
| 12. <i>Phastia maricolor</i> , sp. n.         | Notodontidæ.  |
| 13. <i>Boriza kalodonta</i> , sp. n.          | Notodontidæ.  |
| 14. <i>Hydras albiochrea</i> , sp. n.         | Lasiocampidæ. |
| 15. <i>Sisyrosea guaica</i> , sp. n.          | Limacodidæ.   |
| 16. <i>Plusiodonta cupristria</i> , sp. n.    | Noctuidæ.     |
| 17. <i>Sanys implicata</i> , sp. n.           | Noctuidæ.     |
| 18. <i>Lamontia calibana</i> , sp. n.         | Zygaenidæ.    |
| 19. <i>Bryocodia cryptogramma</i> , sp. n.    | Noctuidæ.     |
| 20. <i>Bryolinna monodonta</i> , sp. n.       | Noctuidæ.     |
| 21. <i>Phostria duplicata</i> , sp. n.        | Pyrilidæ.     |
| 22. <i>Samea delicata</i> , sp. n.            | Pyrilidæ.     |
| 23. <i>Epitomiptera purpurascens</i> , sp. n. | Noctuidæ.     |

48. The Nematode Genus *Physaloptera* Rud.\* By R. J. ORTLEPP, M.A., Research Assistant, Dept. of Helminthology, London School of Tropical Medicine; Hon. Parasitologist to the Society 1921-1922.

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(Text-figures 1-44.)

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### INTRODUCTION.

Rudolphi (1819), when establishing the genus *Physaloptera* expressed some doubt as to its validity. He gives the following as its generic diagnosis:—"Corpus teres elasticum utrinque attenuatum. Os orbiculare. Cauda maris deflexa utrinque alata, vesicam inferam sistens. Penis tuberculo emissus." Dujardin (1845), after quoting Rudolphi's doubt, suppressed the genus and transferred the species to the genus *Spiroptera*. Diesing (1851) re-established the genus, and defined it in such a way that it could not be confused with any other genus of Nematodes. He added two more species, one of which—*Ph. mucronata*—was found to be an Ascarid by Molin.

Leidy (1856) gave a short and incomplete description of four more species, two of which—*Ph. constricta* and *Ph. contorta*—can be definitely ruled out from the genus, as they probably belong to the family *Gnathostomidae* as redefined by Baylis and Lane (1920).

Up to the appearance of Molin's monograph on the genus in 1860, 18 species had been described as belonging to it, namely 9 by Rudolphi, 2 by Creplin, 4 by Leidy, 2 by Diesing, and 1 by Hemprich and Ehrenberg. Of these, 5 are not members of the genus and 1 is doubtful.

\* Communicated by Prof. R. T. LEIPER, F.Z.S.

Molin's monograph contains the descriptions of 22 species, of which 9 are new and 4—*Ph. colubri* (Rud., 1918), Dies., 1851, *Ph. limbata* Leidy, 1856, *Ph. abjecta* Leidy, 1856, and *Ph. spirula* Hempr. & Ehren., 1828—are listed under Species Inquirendæ. In his introduction to this work he eliminates the four species *Ph. strongylina* Rud., *Ph. mucronata* Dies., *Ph. saginata* Rud., and *Ph. tenuicollis* Rud. from the genus, stating that *Ph. mucronata* and *Ph. tenuicollis* are Ascarids, *Ph. saginata* a Spiroptera, and that *Ph. strongylina* belongs to a new genus. He places *Ph. megalostoma* Crep., 1829, as a synonym of *Ph. alata* Rud.

Schneider, in his 'Monographie der Nematoden' (1866), describes 9 species of Physaloptera, of which 4 are new, namely *Ph. digitata*, *Ph. subalata*, *Ph. truncata*, and *Ph. spiralis*. Prior to his publication, and after the appearance of Molin's monograph, the only other new Physaloptera described is *Ph. muris-brasiliensis* Diesing, 1861, from *Mus brasiliensis*.

In 1883, von Drasche amplified Molin's monograph by publishing a revision of the Molin and Diesing types deposited in the Vienna Museum; his work is of considerable value, as he paid special attention to the structure of the lips and caudal extremity of the males, and also gave figures of them all. He confirmed Molin's diagnosis that *Ph. mucronata* Dies., 1851, is an Ascarid.

Von Linstow, in his 'Compendium der Helminthologie' (1878) and in his "Nachtrag" (1889) to this work, records 40 species—31 in the first work and 9 additional ones in the latter.

The next landmark was the appearance of Stossich's monograph on the genus in 1889. He here gave the description of 37 species, 26 of which he considered valid, and the rest he listed under Species Inquirendæ. Those species referred to in this work and not in Molin's are as follows:—1 species—*Ph. torquata*, of Leidy, 1886; 5 species of von Linstow—*Ph. crassa*, 1879, *Ph. dentata*, 1883, *Ph. malleus*, 1883, *Ph. striata*, 1883, and *Ph. pyramidalis*, 1879; 4 species—*Ph. digitata*, *Ph. spiralis*, *Ph. subalata*, and *Ph. truncata*, described by Schneider in 1886; and 1 species of Diesing—*Ph. muris-brasiliensis*, 1861. Of Stossich's 37 species, 11 are recorded from reptiles, 11 from birds, and 15 from mammals.

In 1911, Gedoelst published his 'Synopsis de Parasitologie,' in which he listed 5 species, viz. 2 from man, 1 from carnivores, and 2 from birds.

Hall (1916) gives the descriptions of 7 species, viz. 1 from Hyracoidea, 5 from rodents, and 1, *Ph. abbreviata*, which is a reptilian parasite, but had been recorded from *Graphiurus murinus* by Parona (1909). Hall doubts Parona's diagnosis, and I agree with him that the presence of this parasite in a rodent is very suggestive of an error in its identification.

Up to the present day the number of species has been considerably increased, thanks principally to von Linstow and



Seurat. Von Linstow added 19 species to those of his mentioned above, one—*Ph. amphibia*—being the only record of the occurrence of a member of this genus in amphibians, and another—*Ph. caucasica*—being the first species described from man. Seurat has added 8 new species and two varieties of *Ph. alata*, Rud., 1819.

The latest addition to the literature of this group is two papers by Irwin-Smith reviewing the parasites found in reptiles. In her first paper (1921) she gives a host list of all the reptilian Physaloptera, as well as a bibliographical catalogue in connection with them. In her second paper (1922) she brings together the description of 13 species, all from lizards, and states that of the 15 species recorded from this group of reptiles, only 9, perhaps 10, are valid, the others being either synonyms or not members of this genus.

In Stiles and Hassall's 'Index Catalogue of Round-worms' (1920) 80 species and 2 varieties of Physaloptera are listed, many of which, however, are either synonyms or do not belong to this genus. The addition of 3 species by Gedoelst (1916), 1 by Hall and Wigdor (1918), and 1 by Travassos (1920) not listed in the catalogue, and 7 new species described in this paper brings the number recorded up to 92. These are distributed among the principal host groups as follows:—43 species from mammals, 20 species and 2 varieties from birds, 28 species from reptiles, 1 species from amphibians, and 1 species, *Ph. bonnei*, sp. n., from a host in Dutch Guiana of which its native name is "Sapakara," but of which I have been unable to obtain the scientific name.

The following list comprises all the species recorded from each of these host groups:—

#### AMPHIBIA.

*Ph. amphibia* v. Linst., 1899.

#### REPTILIA.

<i>Ph. abbreviata</i> Rud., 1819.	<i>Ph. longissima</i> , sp. n.
<i>Ph. abjecta</i> Leidy, 1856.	<i>Ph. monodens</i> Mol., 1860.
<i>Ph. affinis</i> Gedoel., 1916.	<i>Ph. mucronata</i> Dies., 1851.
<i>Ph. alba</i> Stoss., 1902.	<i>Ph. obtusissima</i> Mol., 1860.
<i>Ph. aloisii-sabaudie</i> Par., 1907.	<i>Ph. pallaryi</i> Seurat, 1917.
<i>Ph. antarctica</i> v. Linst., 1899.	<i>Ph. paradoxa</i> v. Linst., 1908.
<i>Ph. britanica</i> Skrjabin, 1916.	<i>Ph. phrynosoma</i> , sp. n.
<i>Ph. chamaeleontis</i> Gedoel., 1916.	<i>Ph. quadrovarya</i> Leiper, 1908.
<i>Ph. colubri</i> (Rud., 1819), Dies., 1851.	<i>Ph. retusa</i> Rud., 1819.
<i>Ph. constricta</i> Leidy, 1856.	<i>Ph. simplicidens</i> , sp. n.
<i>Ph. contorta</i> Leidy, 1856.	<i>Ph. sonsinoi</i> v. Linst., 1895.
<i>Ph. dentata</i> v. Linst., 1883.	<i>Ph. spiralis</i> Schn., 1866.
<i>Ph. gracilis</i> , sp. n. [1917.	<i>Ph. striata</i> v. Linst., 1883.
<i>Ph. leptosoma</i> (Gerv., 1848), Seurat,	<i>Ph. varani</i> , Parona, 1889.

## AVES.

- |                                        |                                                |
|----------------------------------------|------------------------------------------------|
| <i>Ph. acuticauda</i> Mol., 1860.      | <i>Ph. inflata</i> (Mol., 1860), Stoss., 1889. |
| <i>Ph. alata</i> Rud., 1819.           | <i>Ph. malleus</i> v. Linst., 1883.            |
| " " v. <i>chevreuxi</i> Seurat, 1914.  | <i>Ph. megalostoma</i> Crep., 1829.            |
| " " v. <i>nouveli</i> Seurat, 1915.    | <i>Ph. ovata</i> v. Linst., 1907.              |
| <i>Ph. bilabiata</i> Crep., 1829.      | <i>Ph. rotundata</i> v. Linst., 1906.          |
| <i>Ph. brevicauda</i> v. Linst., 1909. | <i>Ph. saginata</i> Rud., 1819.                |
| <i>Ph. bulbosa</i> v. Linst., 1906.    | <i>Ph. striata</i> v. Linst., 1883.            |
| <i>Ph. crassa</i> v. Linst., 1879.     | <i>Ph. strongylina</i> Rud., 1819.             |
| <i>Ph. crosi</i> Seurat, 1914.         | <i>Ph. subalata</i> Schn., 1866.               |
| <i>Ph. fusiformis</i> v. Linst., 1902. | <i>Ph. tenuicollis</i> Rud., 1819.             |
| <i>Ph. galinieri</i> Seurat, 1914.     | <i>Ph. truncata</i> Schn., 1866.               |

## MAMMALIA.

- |                                              |                                              |
|----------------------------------------------|----------------------------------------------|
| <i>Ph. anomala</i> Mol., 1860.               | <i>Ph. maxillaris</i> Mol., 1860.            |
| <i>Ph. brevispiculum</i> v. Linst., 1906.    | <i>Ph. mephites</i> Solanet, 1909.           |
| <i>Ph. breviovaginata</i> Seurat, 1917.      | <i>Ph. mordens</i> Leiper, 1908.             |
| <i>Ph. capensis</i> , sp. n.                 | <i>Ph. muris-brasiliensis</i> Dies., 1861.   |
| <i>Ph. caucasica</i> v. Linst., 1902.        | <i>Ph. nasilionis</i> Gedoel., 1916.         |
| <i>Ph. cesticillata</i> , Sons., 1889.       | <i>Ph. numidica</i> Seurat, 1917.            |
| <i>Ph. circularis</i> v. Linst., 1897.       | <i>Ph. papilloradiata</i> v. Linst., 1899.   |
| <i>Ph. citilli</i> (Rud., 1819), Hall, 1916. | <i>Ph. papillotruncata</i> Mol., 1860.       |
| <i>Ph. clausa</i> Rud., 1819.                | <i>Ph. præputialis</i> v. Linst., 1889.      |
| <i>Ph. cælebs</i> v. Linst., 1897.           | <i>Ph. pyramidalis</i> v. Linst., 1879.      |
| <i>Ph. digitata</i> Schn., 1866.             | <i>Ph. rara</i> Hall & Wigdor, 1918.         |
| <i>Ph. dilatata</i> Rud., 1819.              | <i>Ph. ruvenzorii</i> Parona, 1907.          |
| <i>Ph. dispar</i> v. Linst., 1904.           | <i>Ph. semilanceolata</i> , Mol., 1860.      |
| <i>Ph. elegantissima</i> Stoss., 1902.       | <i>Ph. sciuri</i> Parona, 1898.              |
| <i>Ph. gemina</i> v. Linst., 1899.           | <i>Ph. spirula</i> Hempr. & Ehren., 1828.    |
| <i>Ph. getula</i> Seurat, 1917.              | <i>Ph. tacapensis</i> Seurat, 1917.          |
| <i>Ph. guiarti</i> Garin, 1913.              | <i>Ph. terdentata</i> Mol., 1860.            |
| <i>Ph. incurva</i> v. Linst., 1908.          | <i>Ph. torquata</i> Leidy, 1886.             |
| <i>Ph. inermis</i> v. Linst., 1906.          | <i>Ph. torresi</i> (Trav., 1920).            |
| <i>Ph. limbata</i> Leidy, 1856.              | <i>Ph. tumefaciens</i> Henry & Blanc, [1912. |
| <i>Ph. magnipapilla</i> Mol., 1860.          | <i>Ph. turgida</i> Rud., 1819.               |
| <i>Ph. malayensis</i> , sp. n.               |                                              |

## Doubtful Host.

- Ph. bonnei*, sp. n.

## MATERIAL AND ACKNOWLEDGMENTS.

The present work originated in the examination and determination of a number of species of this genus collected by the author at the Prosectorium of the Zoological Society of London, while holding the post of Parasitologist to the Society. Prof. Leiper suggested that the work should be extended, so as to include a redescription of as many as possible of the recorded species of this genus, together with a survey of the whole group. With this aim in view he handed over to me, for study and identification, his valuable collection of Physaloptera, most of which had been personally collected by him during his expedition

to Uganda in 1906. I wish here to express my indebtedness and thanks to the Zoological Society of London for the honour and privilege of collecting these parasites in their Gardens, and to Professor Leiper my sincere thanks and gratitude for having entrusted me with his material, for his valuable advice and criticisms, without which the work could not have been undertaken, and for the use of his valuable library.

In addition to the above material, the writer was able to examine representative material of all of Molin's species, the types of two of Diesing's species, and examples of six of Rudolphi's, including his types of *Ph. clausa* deposited in the Helminthological collection of the Zoologische Abteilung der Naturhistorischen Staatsmuseum, Vienna. I wish to express my indebtedness and thanks to Hofrat Dr. Ludwig von Lorenz-Liburnau, Director of the Zoological Department, for the privilege afforded me to examine this material, and especially also to Dr. Carl Graf Attems, custodian of the Helminthological collection in the Museum, for the excellent facilities so generously placed at my disposal.

Molin did not set apart any material of his species as types, neither did von Drasche when re-examining Molin's material. In consequence of this, I have taken the bottle with the lowest number to represent the type, except in the case of *Ph. obtusissima* and *Ph. terdentata*. In the former case a paratype of the species was examined; in the second case the bottle with the lowest number did not contain Molin's species, but a representative of a later-described species of von Linstow's, namely *Ph. præputialis*; consequently a bottle without any regular number upon it, but with the legend Y1074 on the stopper, was taken as the type; this material had been determined by Molin and also redetermined by von Drasche. The number of the bottles containing what I have taken as the type materials of Rudolphi's, Diesing's, and Molin's species are recorded under the description of the individual species concerned.

The types of the two new species, *Ph. phrynosoma* and *Ph. capensis*, described in this paper will be deposited in the British Museum of Natural History. The types of the five other new species, *Ph. gracilis*, *Ph. longissima*, *Ph. simplicidens*, *Ph. malayensis*, and *Ph. bonnei*, are in the Helminthological Department of the London School of Tropical Medicine.

#### METHODS OF STUDY.

The fresh material obtained from the Prosectorium of the London Zoological Society was collected and washed in normal saline, and as much as possible of the structure of the worms determined while they were still in the living state. They were then killed in hot 70 per cent. alcohol, according to the method recommended by Looss, after which they were preserved in a 70 per cent. alcohol + 5 per cent. glycerine solution. For

further study of this, and the rest of the material it was necessary to render them transparent by some clearing medium. Langeron's lactophenol was at first used, but, although this medium is excellent for small nematodes, it did not give satisfactory results with the larger members of this group, as it did not render the specimen clear enough to make out the details of the spicules. Consequently beechwood creosote was used in its stead. In using this latter medium, the parasites were transferred into strong alcohol, about 95 per cent., and left therein for a longer or shorter period according to the size of the worms; after a sufficient interval to allow for the thorough penetration of this alcohol, they were placed in the creosote and examined, when clear, under the microscope by placing them on a larger slide and rolling them under a coverslip when necessary. After examination it is essential to remove the creosote from the worms, as they tend to become very dark in colour if returned into the preserving fluid without removal of the creosote. To obviate this, the parasites were first immersed for at least two hours in a 1-2 per cent. acid alcohol solution (70 per cent.), after which they could be transferred into the preserving fluid with apparent safety.

All the measurements, except that of the length of the worms, were taken by means of an ocular micrometer, the value of each of whose divisions had been previously determined.

The details of the female genitalia were made out in most species by simple clearing and rolling of the parasites; in the remaining species it was necessary to dissect out these uteri under a dissecting microscope, and to examine them separately when mounted on a slide: where, however, there was ample material of the former, the genitalia were also dissected out.

Where there was sufficient material available, the details of the lips were determined by first cutting the lips off from the body and then examining each lip from the inner and outer surface when cleared and mounted on a slide.

All the figures except one—caudal bursa of *Ph. colubri*—are original. All those accompanied by a scale were drawn by means of a camera lucida; the others are free-hand drawings made from the specimens.

#### GENERAL CHARACTERS OF *PHYSALOPTERA*.

These worms are rounded elongate and taper gradually in their anterior half and posterior third; they vary considerably in size, the largest specimens known being 10 cm. long and nearly 3 mm. thick. The cuticle is loosely attached to the body, and in nearly all cases is extended over the lips to form a prepuce-like collar; in a few species a similar reduplication is present over the caudal extremities of both sexes. The cuticle always shows a very fine transverse striation, which often requires high magnification for its detection.



Two cervical papillæ are present. These are situated laterally a short distance behind the cephalic extremity. They are small and spike-like, and stand out at right angles to the body.

The excretory pore is ventral in position, and is situated a very short distance posterior to the cervical papillæ. It gives exit to a thin duct, which at first passes obliquely inwards and forwards and then bends backwards to join an oval, elongate, and unicellular gland pressed against the ventral surface of the œsophagus.

Two lips are present. These are lateral in position, and have their inner faces flattened and their outer somewhat convex; in lateral view they may be semicircular, dome-shaped, or more or less triangular in outline. They are always simple and their pulp is never subdivided. Each lip carries a variable number of teeth on its anterior and inner border; these consist typically of: (1) an outer median tooth, generally triangular in shape and of variable size; (2) an inner median tooth immediately internal to the outer median: it may be larger, smaller, or of the same size as the outer tooth, and its tip may be either simple and pointed or broadened out and tripartite; (3) two inner lateral teeth, one situated in each of the submedian fields of each lip on its inner surface: they are smaller than the outer tooth and are always split; (4) a series of small denticles arranged in a linear series on the inner surface of the lip, dorsad and ventrad of the median teeth. The external median tooth is always present, but any or all of the other teeth can be absent. Two papillæ are present on the external surface of each lip; these are situated one in each submedian field towards the angles of the lips; they are generally dome-shaped. A number of observers mention the presence of an additional external papilla in the mid-line of the lip. I have not detected any such papillæ in any of the specimens studied, and I am consequently led to the conclusion that a small shoulder-like bulging, sometimes present on the outer surface of the lip, has been mistaken for a papilla.

The œsophagus is a straight and cylindrical organ, increasing slightly in thickness towards its posterior extremity. It is always divisible into two parts, namely, a short, transparent, and slightly thinner anterior muscular portion showing transverse muscular striations, and a posterior glandular portion which is thicker, opaque, and granular. Its lumen is lined with chitin and is triradiate. Seurat mentions the presence of a buccal cavity between the lips and œsophagus. I was not able to detect any such space in my material except in one, *Ph. gracilis*, sp. n., where I think the space was due to contraction; in all my other specimens the œsophagus immediately followed the lips.

The nerve ring is large, and encircles the muscular œsophageal portion in its posterior half.

The intestine is straight, and its connection with the œsophagus is slightly thicker than the rest of the organ, which has a uniform thickness throughout. It opens to the exterior by a



short and oblique rectum, lined internally with chitin and accompanied on its outer surface by a number of rectal glands.

The tail of the female is generally short and conical; it is supplied with a unicellular gland; two lateral caudal pores are present, situated generally behind its middle.

The male caudal extremity is incurved ventralwards, and carries on either side a cuticular expansion, which passes across the ventral surface, some short distance in front of the anus, to join its fellow of the other side. It is always supported by at least four pairs of long pedunculated papillæ, generally arranged circumlocally. Its ventral surface is nearly always ornamented either by longitudinal ridges, or with longitudinal rows of tubercles, or spikes or rounded prominences. In addition, there is present a variable number of ventral papillæ (? absent in *Ph. guianæ* Garin) which are generally sessile; typically these consist of three pre-anal and five pairs of post-anal papillæ, but this number may vary in some species.

In the female the vulva is always situated in the anterior half of the body. It is a circular aperture, generally situated on a slight elevation. It leads into an unpaired ovijectoral portion, which in its turn is followed by a double or multiple portion of the female genitalia. The ovijectoral part consists typically of three subdivisions, viz.: (1) a thick-walled cylindrical and muscular vaginal part, lined internally with chitin; (2) a middle swollen portion, generally having its lumen filled with eggs: this part I have interpreted as "egg-chamber"; and (3) a posterior cylindrical portion of about the same thickness as the vagina, but generally shorter: this part I have designated in the descriptions by the term "common trunk", as it probably represents a fused portion of the uteri. The first two parts are always present, but the last is often absent. The double or multiple parts consist of two or more tubules connected by a thinner part to the common trunk or egg-chamber, and comprising a uterus, a receptaculum seminis, an oviduct, and an ovary. The uteri are large, and are filled with numerous eggs; they fill practically the whole body-cavity, and pass backwards more or less parallel to each other to within a few millimetres from the posterior extremity; they then pass forwards, become thinner, and join on to the receptacula seminis. The receptacula seminis are small, oval, rounded, or pyriform, with their greatest diameter further away from the uteri. The oviducts are fine ducts, connecting the oviducts to the receptacula seminis; their transition into the ovaries is generally gradual, but into the receptacula it is abrupt. The ovaries are long and taper gradually to their tip: they at first pass irregularly forwards, but recurve to end generally in the anterior body half.

The eggs are relatively small, oval, smooth, and very thick-shelled, and are embryonated before being laid.

The male genital tubule is unpaired, and is situated ventrad to the digestive tract. It consists of three well-defined portions,

viz. : (1) a posterior and short but elongately pyriform ejaculatory duct, with its thickest part away from the genital orifice ; (2) a long vesicula seminalis, of the same dimensions throughout and slightly thicker than the ejaculatory duct ; and (3) a much thinner and tapering testis, which passes forwards into the anterior third of the body, after which it recurves, and passes backwards to end at about the middle of the body. The ejaculatory duct and vesicula seminalis are straight, but the testis performs irregular longitudinal loops in its forward course. The accessory male genital apparatus consists of two spicules, of which the left is generally long and slender, and the right shorter and stouter ; they may, however, be of the same length, or the right may be slightly larger than the left.

#### CHARACTERS OF SYSTEMATIC IMPORTANCE.

Seurat (1914) was the first to draw attention to the systematic value of the number of the uteri, and in his writings on the Physaloptera invariably groups his species according to whether they have two or four uteri. In my investigations on this genus I have found also forms possessing as many as 15 uteri, and consequently have classified them into the three groups—Didelphys, Tetradelphys, and Polydelphys.

The number of the uteri and their mode of origin from the ovijector appear to me to be characters of primary systematic value, and the question arises whether they are not of generic significance.

Irwin-Smith (1922) considers it "undesirable to establish a new genus entirely on a character which can be determined only by dissection." I agree with her that it does not appear legitimate to create a genus on only one character ; and consequently I have looked for some other characters common to each of these groups, but have not been able to find any. The whole genus is so compact, and its individual species have so many characters in common, that at the present state of our knowledge of the Physaloptera, I am compelled to retain them all in the same genus, however much I have felt inclined to split them up for the sake of convenience.

Travassos (1920) separates from the genus *Physaloptera* four new genera, limiting the genus *Physaloptera* to those forms possessing similar and subequal spicules, two uteri, four pairs of pedunculated papillæ, and having no reduplication of the cuticle over the caudal extremity. He gives the following key to these five and three other nearly related genera :—

#### 1. Spicules similar and subequal.

##### A. Two uteri.

- a.* Four pairs of pedunculated papillæ ; no prepuce-like sheath at the posterior extremity ..... *Physaloptera.*
- b.* A prepuce-like collar present at the posterior extremity ... *Chlamydonema.*
- c.* Eight pairs of pedunculated papillæ..... *Thubunæa.*

##### B. Ten uteri ... *Turgida.*

2. Spicules dissimilar, and their sizes very different.

AA. Two uteri.

aa. Four pairs of pedunculated papillæ ..... *Abreviata*.

bb. Nine to ten pairs of pedunculated papillæ.

cc. Vulva in anterior half; ovjector very long ..... *Heliconema*.

dd. Vulva near to the anus ..... *Proleptus*.

BB. Four uteri ..... *Leptosoma*.

Except for the genus *Turgida*, Travassos gives no generic diagnoses for his new genera, so that in order to form a conception of the three genera *Chlamydonema*, *Abreviata*, and *Leptosoma*, we are limited to the skeletal framework of his key. He also does not indicate which species he regards as the type of each of these three genera, but as he has used the term *Turgida* in raising the species *Ph. turgida* to generic rank, I take it that *Chlamydonema* will have as its type-species *Ph. præputialis* von Linstow, 1899, because *Chlamydonema felineus* is the name used by Hegt (1910) in describing a nematode parasite from the Domestic Cat, being apparently unaware of its physalopteran characters or its identity with *Ph. præputialis*. *Abreviata* is presumably Rudolphi's species *Ph. abbreviata* raised to generic rank, and *Leptosoma* is presumably *Ph. leptosoma* (Gervais) Seurat, 1917, raised to a new genus.

In view of Seurat's investigations and my own observations on the genus *Physaloptera*, all Travassos' genera appear to me to be untenable. *Chlamydonema*, besides the characters it has in common with Travassos' restricted genus *Physaloptera*, has in addition the prepuce-like collar over the posterior extremity; now, *Ph. tumefaciens* Henry & Blanc, 1912, also shows this characteristic, although not to such a marked extent as in *Ph. præputialis*, but as it has four uteri, it cannot be included in the genus *Chlamydonema*, so that this genus is not valid.

The genus *Turgida* has all the characters of the genus *Physaloptera* as restricted by Travassos, except that it is polydelphoid, so that its validity is based on this single characteristic. As shown above, I do not regard the multiplication of the uteri by itself as of more than specific value. *Ph. capensis*, sp. n., is also polydelphoid, but the mode of origin of its uteri is quite different from that in *Ph. turgida*, so that if the genus *Turgida* is accepted, then a special genus would have to be created for *Ph. capensis*, a procedure which I consider quite unjustifiable.

*Ph. abbreviata*, as redescribed by Seurat (1914 b), has four uteri, so that on this ground alone the genus *Abreviata* must be suppressed, as Travassos creates it for those forms possessing two uteri and having very equal and dissimilar spicules; besides, the tetradelphoid species *Ph. tumefaciens* and *Ph. magnipapilla* have only slightly unequal spicules, which character also does not tally with Travassos' conception of his new genus.

The genus *Leptosoma*, according to Travassos' key, is characterised by having four uteri and very unequal and dissimilar

spicules. According to Seurat (1917 *a*), who has studied *Ph. leptosoma*, this species has only two uteri, so that again it appears that Travassos has made a new genus on wrong data. At any rate the name *Leptosoma* is not available, as according to Scudder (1882) it has already been used by Leach (1819) for a beetle, by Risso (1826) for a crustacean, by Nardo (1827) for a fish, and by Boisd. (1833) for a lepidopteran, while the form *Leptosomus* was used by Vieill. (1816) for a bird, and by Schönh. (1826) for a coleopteran.

With regards to the genera *Thubuncea* Seurat, 1914, *Heliconema* Trav., 1919, and *Proleptus* Duj., 1845, it does not appear necessary to discuss them here, as they do not affect the status of the genus *Physaloptera*.

Seurat (1915-16) has also proposed dividing the genus into four groups according to the teeth. These groups he characterises briefly as follows:—

1st group of *Ph. galinieri* Seurat.

The internal median tooth tripartite and very large, passing over the small external tooth.

2nd group of *Ph. clausa* Rud.

The external and median teeth are of the same height.

3rd group of *Ph. alata* Rud.

The external tooth is very large and triangular; the internal tooth (tripartite) is small.

4th group of *Ph. abbreviata* Rud.

The external tooth is enormous and triangular; the internal tooth is very small and difficult to see.

If we adopt this division, we would be obliged to add a 5th group of *Ph. colubri* (Rud.), Dies., characterised by the presence of a large and triangular external tooth and the entire absence of the internal median tooth.

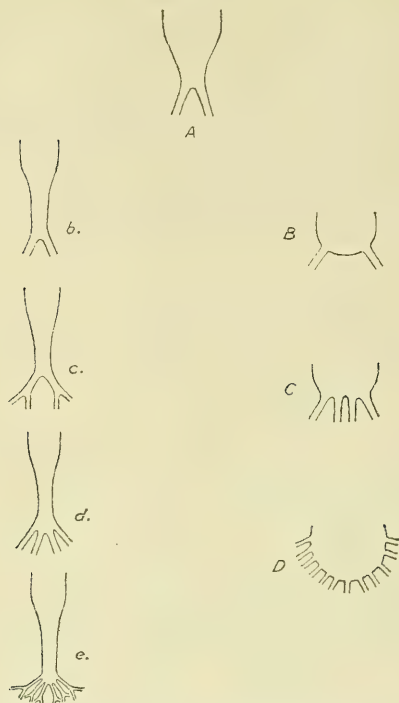
In subdividing any group of animals, our first aim is to bring together those forms which possess close affinities to each other, and not those forms which, when grouped together, render it easier or more convenient to us to determine them. Seurat's divisions, when submitted to this test, are consequently not tenable, as it would imply that all the polydelphoid forms are closely related to such didelphoid forms as *Ph. preputialis* and *Ph. maxillaris*.

Assuming that the line of evolution has proceeded from the didelphic to the polydelphic forms, then, I think, we have to recognise two ways, both starting from a form with genitalia of the *Ph. clausa* (text-fig. 1 A) type. The one group would evolve from this type through stages like *Ph. preputialis* (text-fig. 1 B), *Ph. tumefaciens* (text-fig. 1 C) to *Ph. turgida* (text-fig. 1 D), and



the other along such stages as *Ph. obtusissima* (text-fig. 1 *b*), *Ph. abbreviata* (text-fig. 1 *c*), *Ph. paradoxa* (text-fig. 1 *d*) to *Ph. capensis* (text-fig. 1 *e*).

Text-figure 1.



Schematic representation of the probable methods of Uterine evolution from the didelphoid to the polydelphoid conditions.

A = *Ph. clausa* type; B = *Ph. præputialis* type; C = *Ph. tumefaciens* type;  
D = *Ph. turgida* type; b = *Ph. obtusissima* type; c = *Ph. abbreviata* type;  
d = *Ph. paradoxa* type; e = *Ph. capensis* type.

For the specific determination of the material examined, the following characters were especially noted:—

1. Number of uteri and their mode of origin.
2. Number and arrangement of the male caudal papillæ.
3. Relative lengths and shape of the spicules.
4. Number, shape, and size of the labial teeth.
5. Cuticular markings on the ventral surface of the male bursa.
6. Position of the vulva.



7. Presence or absence of a cuticular sheath at the posterior extremity.
8. Size of the eggs.
9. Relative length of the œsophagus.
10. Positions of the excretory pore and cervical papillæ.

The value attaching to each of these characters is indicated by its position in the above list.

#### SYSTEMATIC SECTION.

The remainder of the paper is divided into two parts. Part I. contains the descriptions and diagrams of all the species personally studied. Part II. gives an extract of the principal characteristics of all the species not personally examined. In most cases these extracts are based on the original descriptions and drawings; where this is not the case, the source is recorded under the species concerned. In each part the parasites are classified into three groups according to whether they were di-, tetra-, or polydelphoid, the arrangement proceeding from Mammals to Birds and to Reptiles.

*Ph. acuticauda*, however, has been placed together with *Ph. præputialis* and *Ph. malayensis* after the reptilian didelphoid forms, because of the similarity of their female genitalia. Species Inquirendæ, and species which were described as belonging to the genus *Physaloptera* but which have since been found to have been misplaced, are listed at the end of Part II.

The hosts cited after the species in Part I. are the hosts from which the material examined was collected; the hosts in Part II. are those from which the material collected formed the basis of the descriptions. A more detailed list of hosts from which the separate species have been recorded is furnished by Stiles and Hassall's 'Index Catalogue of Round-worms' (1920).

#### PART I.

##### Generic Diagnosis (emended).

Superfamily *SPIRUROIDEA*.

Family *PHYSALOPTERIDÆ*.

Subfamily *PHYSALOPTERINÆ*.

Mouth with two large simple and lateral lips, each armed with a variable number of teeth and carrying two external papillæ. Œsophagus consists of an anterior muscular and a posterior glandular part. Cuticle generally reflected over the lips. Caudal extremity of male with lateral alæ joining each other across the ventral surface in front of the anus. At least four pairs of pedunculated papillæ supporting the alæ; these generally arranged circumlocally. A variable number of ventral caudal papillæ,

generally three pre-anal and five pairs post-anal. Spicules unequal, subequal, or equal. Vulva in anterior half of body. Two, four, or many uteri. Eggs oval, smooth, thick-shelled, and embryonated when laid.

Parasitic normally in the digestive tract, generally the stomach, of mammals, birds, and reptiles, but very rarely in amphibians.

Type-species, *Ph. clausa* Rud., 1819.

### GROUP *Didelphys*.

(1) *PHYSALOPTERA CLAUSA* Rudolphi, 1819. (Text-figs. 2-4.)

Syn. *Spiroptera clausa* (Rud.), Duj., 1845.

The material examined consisted of many specimens from *Erinaceus europæus* in the Vienna Museum (bottles 4447 & 4450), also some specimens from the same host in the collection of Prof. R. T. Leiper. The three lots of material were in all respects identical.

The cuticle appears smooth, but under high magnification a very delicate transverse striation is seen; it is only very slightly reflected over the base of the lips.

The cervical papillæ are lodged in small depressions of the cuticle, and are situated from 115 to 165  $\mu$  behind the level of the hind end of the muscular œsophagus; the excretory duct opens in the ventral mid-line at the same level as the cervical papillæ or just behind them.

The lips are almost semicircular in lateral view, but appear square in dorsal or ventral view. Each bears a medium-sized conical outer tooth with obtuse tip, and just internal to it a median tooth of equal height with three tips to its free end. No lateral teeth are present. The subdorsal and subventral external papillæ are small and dome-like.

The œsophagus immediately follows the lips; it is straight, and forms in the female 1/7·8 to 1/9th, and in the males 1/5·4 to 1/5·6 of the total body-length. Its muscular part is distinctly set off from the glandular, and is also slightly thinner; in the females it forms about 1/8·5, and in the males 1/7th of the whole organ. The nerve ring encircles it in its posterior quarter.

#### *Female.*

Mature females vary in length from 30 to 50 mm., with a maximum thickness of 1·3 to 1·6 mm. The body is attenuated in its anterior 1/3rd and posterior 1/5th; it is terminated by a bluntly conical tail 1/45th to 1/55th of the total body-length, with caudal pores in its posterior half.

The position of the vulva divides the body in the ratio of 1:1·7 to 1:2; it is situated on a slight elevation, and leads into a bent vagina 1·6 mm. long by 95  $\mu$  broad; the egg-chamber is slightly shorter but thicker, measuring 1·3 mm. long by 325  $\mu$  broad. From its posterior end the uteri, of which there are two,

directly take their origin, so that a common trunk portion is absent.

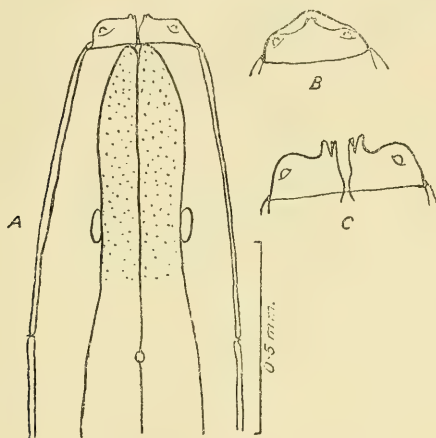
The eggs are oval and thick-shelled, measuring  $52\mu$  long by  $38\mu$  broad.

### Male.

The males varied in length from 15 to 28 mm., with a breadth of 825 to 875  $\mu$ . The body is attenuated only on its anterior half.

The caudal bursa is large, forming about 1/11th of the total length; it is bluntly rounded posteriorly, and is closely coiled ventralwards. The lateral expansions are well developed, and

Text-figure 2.



*Physaloptera clausa* Rud.

A = Anterior extremity of body.

B = Externo-lateral view of lip.

C = Ventral view of lip.

the four pairs of pedunculated papillæ supporting them are equidistant, two pairs being pre-anal and two pairs post-anal. There are 13 ventral papillæ, of which three are pre-anal and the rest post-anal. The pre-anal papillæ are situated in a row immediately anterior to the anus, the middle papilla being larger than the other two. The first two pairs of post-anal ventral papillæ are small and situated in a row just behind the anus; the remaining papillæ are equidistant and large, and they divide the tail into quarters; in some cases the last two pairs may be slightly approximated to each other.

The left spicule is nearly half as long again as the right, and is also much slenderer; it is  $740\mu$  long by  $33\mu$  broad at

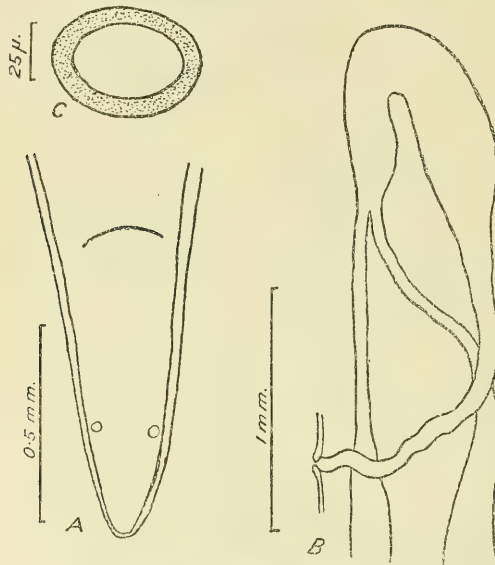
its base and tapers to a fine point; the right spicule is stout,  $495\ \mu$  long and  $50\ \mu$  broad at its base, and also terminates in a fine point.

Host: *Erinaceus europæus*. Stomach. Europe.

Types in bottle 4447 in the Vienna Museum.

My observations on this species differ in many respects from those of Seurat (1917*b*) made on worms obtained from *Erinaceus algirus* and *Erinaceus deserti*. These differences apply more especially to the male. Seurat finds that of the three pre-anal ventral caudal papillæ the two lateral ones are far removed from

Text-figure 3.



*Physaloptera clausa* Rud.

A = Caudal extremity of female.

B = Terminal parts of female genitalia.

C = Egg-shell.

the median papilla and are also stalked; in my material these three papillæ are situated close together in a line immediately in front of the anus, and the lateral papillæ are non-pedunculate; also the median papilla is large and nearly twice the size of the other two, whereas Seurat finds this papilla to be very small.

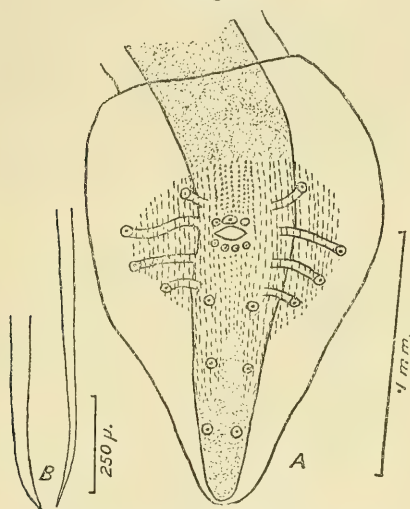
With regard to the post-anal ventral papillæ, the third pair is stalked in Seurat's material and sessile in mine.

Further, the spicules of his specimens differ from those of mine both in length and in shape; in his material the right and

left spicules are respectively 300 and 360  $\mu$  long, and only the left has a pointed tip. In my material the spicular lengths are as follows: right 495  $\mu$ , left 740  $\mu$ , *i. e.* the right is more than half as long again and the left twice as long. Both of them terminate in sharp points.

These, besides other minor differences, *e. g.* size of egg, length of ovijector, position of the vulva, etc., seem to indicate that the specimens studied by me belong to different species; and as I examined what I take to be the type-material, I think Seurat's specimens must be regarded as a new species, which, however, is very closely allied to *Ph. clausa*, as shown by the nature of the teeth and mode of origin of the two uteri.

Text-figure 4.

*Physaloptera clausa* Rud.

A = Caudal extremity of male.    B = Spicules.

Schneider (1866) states that the inner teeth are smaller than the outer, and figures a male bursa having the papillæ arranged very similarly to those figured by Seurat; he does not definitely state that he has examined the Vienna material, although he quotes the same host from both Vienna and Berlin; it is probable that he examined material only from the latter locality, and that would partly account for the differences between his and my observations; it is therefore probable that he also is not dealing with *Ph. clausa*, but with a species identical with or very closely allied to that described by Seurat. Unfortunately Schneider's description is very brief, so that I am not able to make a closer comparison between his and Seurat's accounts.



(2) *PHYSALOPTERA PAPILLOTRUNCATA* Molin, 1860. (Text-fig. 5.)

The material examined consisted of the types of the species deposited in the Vienna Museum; this material had also been examined by von Drasche.

The cuticle is very finely striated transversely, and in the specimens examined it was not reflected over the lips; a coarse ringing is present in some specimens, probably due to some shrinkage.

The cervical papillæ are situated from 150 to 250  $\mu$  behind the level of the posterior margin of the muscular œsophagus, and the excretory duct opens to the exterior either at the same level or about 75  $\mu$  further back.

The lips are hemispherical in lateral view, and each has only two teeth, namely a large and blunt outer tooth recurved outwards, and a smaller tripartite inner tooth. Each lip bears on its subdorsal and subventral outer surface a dome-like papilla.

The œsophagus is straight, and forms in the females from 1/5.6 to 1/7th, and in the males 1/5th of the total body-length. Its muscular part is slightly thinner than the following glandular part, and forms from 1/8.6 to 1/10th of the whole organ; it is encircled by the nerve ring at the junction of its fourth and last fifths.

*Female.*

The females examined varied in length from 32 to 68 mm., with a maximum breadth of from 1 to 2.1 mm. The body is much attenuated in its anterior half, and slightly less so in its posterior quarter, where the body is terminated by a short and truncated tail 1/66th to 1/80th of the total body-length; its caudal pores are situated just behind its middle.

The vulva opens on a slight elevation, and is situated relatively far back; it divides the body in the ratio of 1:1.8 to 1:1.2; it leads into a slightly curved and muscular vagina 1.5 mm. long by 96  $\mu$  broad; this passes into the egg-chamber, which is 1.3 mm. long by 210  $\mu$  broad. The trunk which follows is of the same length and breadth as the vagina; from its posterior end there arise the two uteri which at first pass forwards, but soon recurve and pass down the length of the body.

The eggs are oval and thick-shelled, measuring on the average 52  $\mu$  long by 30  $\mu$  broad.

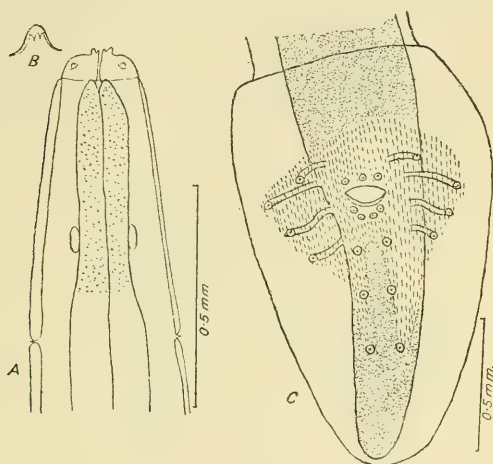
*Male.*

The males are much smaller than the females, and are attenuated in their anterior third, the rest of the body being of about the same thickness; they vary in length from 20 to 25 mm. with a breadth of 750 to 800  $\mu$ .

The bursa is large, and forms about 1/10th of the body-length; it has well-developed cuticular expansions, and is rounded at its tip. The ventral surface is traversed by longitudinal rows of protuberances. The four pairs of stalked papillæ are equidistant

from each other, the first, however, being more ventral in origin; two pairs are pre-anal, and the other two pairs are post-anal in position. The three pre-anal ventral papillæ are situated in a row immediately in front of the anus. There are five pairs of post-anal papillæ, of which pairs 1 and 2 are small and situated close together immediately behind the anus, one pair being slightly more posterior than the other; pairs 3, 4, and 5 are equidistant from each other; the distance between the 2nd and 3rd pairs is about half that between the 3rd and 4th pairs, and the distance between the 5th pair and the tip of the tail is about twice that between the 4th and 5th pairs.

Text-figure 5.

*Physaloptera papillotruncata* Mol.

A = Cephalic extremity of body.

B = Inner view of median labial teeth.

C = Caudal extremity of male.

The spicules are equal and straight; the right spicule is slightly slenderer than the left, and ends in a sharp point; the end of the left spicule is slightly flattened out to form a small spear-head; they are  $360\ \mu$  long by  $35$  and  $38\ \mu$  thick at their base respectively.

Host: *Myrmecophaga jubata*. Stomach. Brazil.

Types in bottle 4477 in the Vienna Museum.

Discussion.—See *Ph. maxillaris*.

### (3) PHYSALOPTERA SEMILANCEOLATA Molin, 1860. (Text-fig. 6.)

The material examined was somewhat shrunken, but in excellent preservation.

The cuticle is finely striated, and shows, in addition, an

irregular course ringing, probably due to contraction; in some cases it is completely reflected over the lips, and in others only the base of the lips are covered.

The cervical papillæ are situated about  $300\ \mu$  behind the level of the hind end of the muscular œsophagus, and the excretory duct opens about  $90\ \mu$  further back.

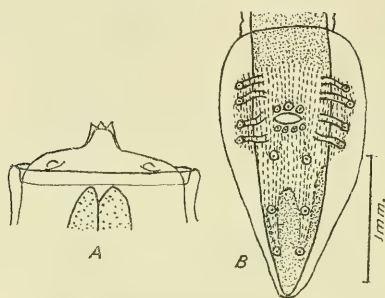
In the specimens examined the œsophagus was thrown into loops, so that a correct estimation of its length could not be determined; roughly, it forms in the male about  $1/5$ th, and in the female about  $1/6$ th of the total length.

The lips are flatly rounded, and each bears two large terminal teeth of the same height; the outer tooth is markedly truncated, whereas the inner is foliaceous and tripartite. Each lip has on its outer surface a prominent subdorsal and subventral papilla.

#### *Female.*

The females are coiled, and mature specimens average in length from 21 to 37 mm. long by  $\cdot 9$  to 1.5 mm. thick. The body is of

Text-figure 6.



*Physaloptera semilanceolata* Mol.

A = Externo-lateral view of head.

B = Caudal extremity of male.

a more or less uniform thickness throughout, except for the anterior  $1/10$ th and posterior few millimetres. The tail in all specimens examined was bent dorsalwards. It tapers only slightly towards its tip, which is very bluntly rounded; the caudal pores open in its posterior  $1/5$ th.

The vulva opens very far forwards, in some specimens its position being just anterior to the hind end of the œsophagus and in others just behind it. It leads into a long and coiled vagina about 3 mm. long by  $110\ \mu$  broad; its posterior end gradually widens to join the swollen egg-chamber, which, when distended with eggs, measured 2.75 mm. long by  $440\ \mu$  broad. The common trunk is relatively short and slightly thinner than the vagina; it measured about  $475\ \mu$  long by  $95\ \mu$  thick. The two uteri which arise from it may first pass forwards, and then recurve to pass down the length of the body.

The eggs are oval and thick-shelled, and are already embryo-nated *in utero*; they are  $50\ \mu$  long by  $32\ \mu$  broad.

*Male.*

The males are also coiled, and the body is attenuated in its anterior third. The specimens examined measured from 25 to 32 mm. long by 750 to  $875\ \mu$  thick. The bursa is relatively narrow and pointed, and three of the four pairs of pedunculated papillæ are pre-anal in position. The three pre-anal ventral papillæ are equidistant from the cloaca, and the central papilla is slightly larger. There are five pairs of post-anal ventral papillæ, of which the first two pairs are small and situated in a row immediately behind the anus; the third pair is at the junction of the 1st and 2nd sixths of the tail, the fourth at about the middle, and the last at the junction of the 3rd and last quarters of the tail. The ventral surface is covered with longitudinal rows of irregular tubercles.

The spicules are slightly unequal, of the same thickness, and slightly curved; both taper to fine points; the right is  $574\ \mu$  long by  $38\ \mu$  thick at its base, the left is  $730\ \mu$  long by  $38\ \mu$  at its base.

Host: *Nasua narica*. Stomach. Brazil.

*Discussion.*—The small pair of papillæ between the 4th and 5th pairs of ventral post-anal papillæ described by von Drasche are the openings of the caudal pores.

*Affinities.*—See *Ph. maxillaris*.

(4) PHYSALOPTERA MAXILLARIS Molin, 1860. (Text-fig. 7.)

The material examined consisted of the types of this species deposited in bottle 4458 in the Vienna Museum; the material was in an excellent state of preservation.

The cuticle is finely striated transversely, and is partly or wholly reflected over the lips. The cervical papillæ are situated half a millimetre behind the junction of the two œsophageal parts, and the excretory pore about  $50\ \mu$  further back.

The lips are rounded or slightly conical; each has two terminal teeth—namely, a large triangular outer tooth with obtuse tip slightly bent outwards, and an inner semi-membranous tooth, tripartite at its free end, and of the same size as the outer tooth. Two large conical papillæ are present on the outer surface of each lip.

The œsophagus is straight, and thickens gradually towards its posterior end; in the female it forms  $1/5.2$  to  $1/5.4$ , and in the male  $1/6$ th to  $1/6.4$  of the body-length; its anterior tenth forms the muscular part, which is slightly thinner than the glandular, and is encircled by the nerve cord in its posterior third.

*Female.*

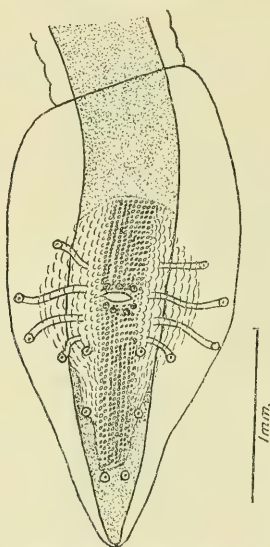
The females are stout, and are attenuated only in their anterior third and tail region; this latter part tapers abruptly to form a short and pointed tail  $1/73$ rd of the body-length, and having its caudal pores situated in its middle. Mature forms vary in

length from 20 to 36 mm., with a maximum breadth of  $800\ \mu$  to 1.24 mm.

The vulva is slightly protuberant, and its position divides the body into the ratio of 1:1.6. The vagina is long, and varies in length from  $2\frac{1}{4}$  to  $3\frac{1}{4}$  mm. with a thickness of  $95\ \mu$ . The egg-chamber is elongately oval, and is 1.7 mm. long by  $435\ \mu$  in diameter. The common trunk is short, and varies in length from 290 to  $320\ \mu$ ; it is slightly thicker than the vagina; from its posterior end the two uteri take their origin, and may either pass forwards and then bend backwards, or else pass posteriorly directly.

The eggs are oval and thick-shelled, and measure  $43\ \mu$  long by  $31\ \mu$  broad.

Text-figure 7.



*Physaloptera maxillaris* Mol.

Caudal extremity of male.

#### Male.

The males are much attenuated from behind forwards, having their maximum thickness just above the bursa; they vary in length from 23 to 32 mm., with a thickness of 550 to  $800\ \mu$ .

The bursa is elongated and somewhat pointed, and has its caudal expansions well developed in its middle portion. Its ventral surface is ornamented by two types of cuticular bosses, those in the central area, above and below the anus, being rounded, simulating those found in *Ph. præputialis*, while those on the lateral areas are in the form of much-broken ridges; the transition from the one type to the other is gradual.



The four circumloacal lateral papillæ are provided with very long stalks, especially the 2nd and 3rd pairs. The ventral papillæ in the immediate vicinity of the anus are small, and consist of three pre-anal papillæ in a row, and two pairs post-anal, also in a row. Further down the tail there are three additional pairs; these are equidistant from each other, the most anterior being situated just behind the level of the last pair of stalked papillæ.

The spicules are slightly bent, unequal; and the right is stouter than the left; both taper to sharp points. The left is 1.2 mm. long by  $40\mu$  thick at its base, and the right is  $560\mu$  long by  $57\mu$  thick at its base.

Host: *Mephites chinche*. Stomach. Brazil.

Types in bottle 4458 in the Vienna Museum.

Some specimens of this species, collected from *Mephites mephitica*, were handed over to me for identification by Mr. R. I. Pocock, F.R.S.; he obtained them from animals introduced into Northumberland (England) from Canada, but how long they had been in England before the parasites were collected it was not possible to definitely find out. I wish to express my thanks to Mr. Pocock for this material.

This material differs from the types studied in that they are slightly larger, and the bursa of the male appears rounded and lobulated; however, I believe these characters of the bursa to be due to shrinkage, as the worms had been killed in formalin.

Solanet in 1909 described another species—*Ph. mephites*—from *Mephites suffocans*, Buenos Aires. Unfortunately I have not been able to consult his description, and consequently cannot discuss the relation of this species to *Ph. maxillaris*.

The arrangement of the ventral bursal papillæ, the presence of two uteri, general characters of the teeth, ally this species to *Ph. semilanceolata*, *Ph. clausa*, and *Ph. papillotruncata*. *Ph. semilanceolata* differs from it by its truncated outer tooth, more anterior position of the vulva, shorter left spicule, and type of ornamentation on the bursa. It differs from *Ph. papillotruncata* by its longer and pointed spicules, ornamentation on the bursa, and smaller size of the adult females. *Ph. clausa* is distinguished from it by the size of the spicules, markings on the bursa, and absence of a common trunk to the unpaired female genitalia.

(5) PHYSALOPTERA ANOMALA Molin, 1860. (Text-fig. 8.)

The material examined consisted of three males and one female; type-material in bottle 4446 in the Vienna Museum. The material was in excellent preservation.

The cuticle is finely striated transversely, and is partly reflected over the base of the lips; the cervical papillæ pierce it on either side from 320 to  $400\mu$  behind the level of the posterior end of the muscular œsophagus; the excretory pore is found about  $100\mu$  further back.

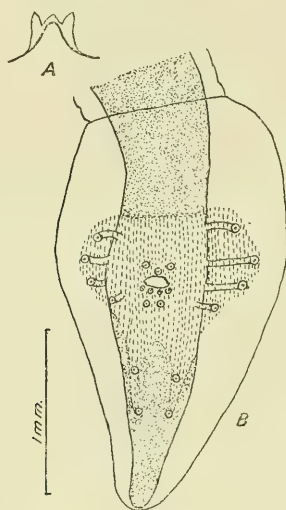
The lips are large and conical, and each carries a large conical but blunt tooth; the inner tooth is large and of equal height, with its free end divided into three points, of which the middle one is slightly shorter than the other two. No lateral teeth are present. Externally each lip carries a subdorsal and subventral conical papilla.

The œsophagus has its anterior muscular part thinner than the rest, and the nerve ring encircles this part in its posterior quarter. The œsophagus forms in the male about  $1/5.4$ , and in the female  $1/5.6$  of the total body-length.

*Female.*

The solitary female was 36 mm. long and just under 2 mm.

Text-figure 8.



*Physaloptera anomala* Mol.

A = Outer view of median teeth.

B = Caudal extremity of male.

broad in its middle; the body is much attenuated in the anterior half, but only slightly so posteriorly; it is terminated by a bluntly-pointed tail,  $1/60$ th of the body-length, and having the caudal pores in its posterior half.

The vulva is situated just behind the end of the œsophagus, and divides the body in the ratio of  $1:4.2$ ; it leads into a coiled vagina 1.9 mm. long by  $95\mu$  thick; this joins with a large and spacious egg-chamber 2 mm. long by  $560\mu$  broad, which posteriorly narrows suddenly to join the  $400\mu$  long common trunk, which is of the same thickness as the vagina. The posterior end

of the trunk divides into two branches, each of which connects up with one of the two uteri.

The eggs are thick-shelled and oval, measuring  $38\ \mu$  long by  $26\ \mu$  broad.

#### Male.

The males are from 30 to 32 mm. long by 1 to 1.2 mm. broad; they are attenuated towards both extremities and the bursa is slightly incurved.

The caudal bursa is large, and is covered ventrally by longitudinal rows of cuticular elevations. The four pairs of pedunculated papillæ are situated three pairs pre-anal and a pair post-anal. Of the three pre-anal ventral papillæ the middle one is nearer the anus. There are five pairs of post-anal papillæ, of which the pairs 1 and 2 are small, and situated in a row immediately behind the anus. Pairs 4 and 5 are large, and are situated in the middle area of the tail. The distance between the 3rd and 4th pairs is about four times the distance between the 2nd and 3rd pairs, and twice that between the 4th and 5th pairs.

The spicules are short and equal, each measuring  $495\ \mu$  long by  $32\ \mu$  broad at their base; they are straight, tubular, and pointed.

Host: *Felis onca*. Stomach. Brazil.

Types in bottle 4446 in the Vienna Museum.

(6) PHYSALOPTERA MURIS-BRASILIIENSIS Diesing, 1861. (Text-fig. 9.)

Syn. *Spiroptera bilabiata* Mol., 1860 (not *Spiroptera bilabiata* (Crep., 1829), Duj., 1845).

The material studied consisted of ten females in bottle 4525 and two males in bottle 4524 in the Vienna Museum. This material constituted the types of this species.

The cuticle forms a ring round the base of the head, but leaves the lips naked; it is very finely striated transversely. The cervical papillæ are situated about  $250\ \mu$  behind the level of the hind end of the muscular œsophagus, and the excretory pore is situated about  $100\ \mu$  further back.

The lips are large, and each bears two large outer papillæ. The external tooth is small, and the inner is of the same size, foliaceous, and tripartite; no additional teeth were observed.

The muscular œsophagus is markedly thinner than the rest of the organ, and forms a little less than 1/10th of its whole length. The nerve ring encircles it in its posterior 1/4th. The œsophagus forms in the female about 1/8th and in the male about 1/6th of the total body-length.

#### Female.

The length of the female varies from 35 to 43 mm., with a maximum breadth of 1.1 to 1.75 mm.

The body is attenuated in its anterior third, but posteriorly has a more or less uniform thickness; it is terminated by a short and obtusely rounded tail, forming about 1/100th of the total body-length.

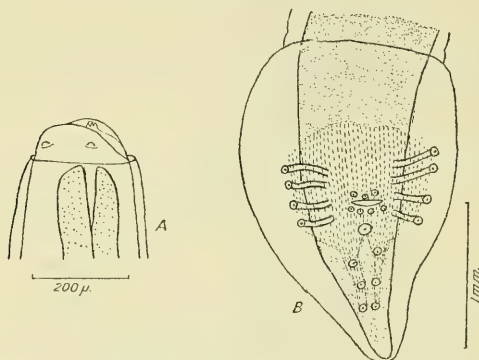
The vulva is slightly protuberant, and is situated at about the junction of the first and second quarters of the body. It leads into a coiled vagina 2 mm. long by  $80\mu$  thick; the egg-chamber is about  $800\mu$  long by  $300\mu$  thick and the common trunk about  $640\mu$  long by  $112\mu$  broad; its posterior end divides into two to give rise to the two uteri.

The eggs are oval and thick-shelled, measuring  $45\mu$  by  $26\mu$  broad, and are fully embryonated *in utero*.

#### Male.

The two males were respectively 22 and 28 mm. long, with a thickness of 870 and  $950\mu$ . They are attenuated in their anterior half and the posterior end is curved ventralwards,

Text-figure 9.



*Physaloptera muris-brasiliensis* Dies.

A = Anterior extremity of male.

B = Caudal extremity of male.

The bursa is somewhat heart-shaped with a drawn-out tip, the lateral expansions being much better developed in their anterior half. Of the four pairs of pedunculated papillae three pairs are pre-anal. There are six pairs of ventral paired papillae and two unpaired papillae; of these one pair and an unpaired papilla are pre-anal, the latter being nearer the anus. The first and second pairs of post-anal papillae are small and are situated in a row immediately behind the anus; pairs 3, 4, and 5 are equidistant from each other, and are situated respectively at the 2nd, 3rd, and 4th sixths of the tail; they are all larger than the first two pairs. The unpaired post-anal papilla is about midway between the 2nd and 3rd pairs, and is about twice as large as the latter.



The spicules are equal, straight, and pointed, each measuring  $400\ \mu$  long by  $32\ \mu$  broad.

Host: *Mus brasiliensis*. Stomach and small intestine. Brazil.

Type males in bottle 4524, type females in bottle 4525, both in the Vienna Museum.

Von Drasche, in his account of this species, considers that the number and arrangement of the bursal papillæ may be somewhat different, as the material he worked with was too opaque. By clearing the specimens in beechwood creosote, I was able to make out two additional pairs of ventral post-anal papillæ, viz. pairs 2 and 4, as well as the nature and lengths of the spicules.

(7) PHYSALOPTERA ALATA Rudolphi, 1819. (Text-fig. 10.)

Syn. *Spiroptera physalura* Duj., 1845.

The material examined consisted of some males and females from *Falco gallicus* and some females from *Falco pennatus*; both lots from the Vienna Museum.

These parasites have a somewhat slender body, whose cuticle is very finely striated transversely; the cuticle is either completely reflected over the lips or else leaves them quite naked.

The cervical papillæ are found from  $75$  to  $100\ \mu$  behind the level of the hind end of the muscular œsophagus. The position of the excretory pore appears to vary in that it was found in some specimens to be very slightly posterior to the cervical papillæ, whereas in others it was as much as  $200\ \mu$  further back.

The lips are somewhat spherical in lateral view, and each carries two terminal teeth; the inner median tooth consists of three large denticles, and is larger than the outer tooth; the outer tooth varies in size: in some specimens it is very small, whereas in others it is almost as large as the inner tooth; a series of sizes can, however, be traced in different specimens, showing the transitions of the smaller to the larger sized outer teeth. Two somewhat slender external papillæ are present on each lip.

The œsophagus is straight, and forms in the males about  $1/6$ th and in the female  $1/5.3$  to  $1/6.6$  of the body-length. Its muscular part is thinner than the glandular, and is encircled by the nerve ring in its posterior quarter; it forms about  $1/9$ th of the whole organ.

*Female.*

The females from *F. gallicus* were all immature except one, and this specimen was 21 mm. long and  $540\ \mu$  thick; those from *F. pennatus* were about 30 mm. long and  $700\ \mu$  thick, and were all mature; the body is attenuated in its anterior half and also slightly in its posterior third; in the immature forms the tail forms about  $1/45$ th of the body-length, but in the mature forms it is slightly longer.

The vulva opens practically level with the general surface, and is situated relatively far back; its position varies slightly,



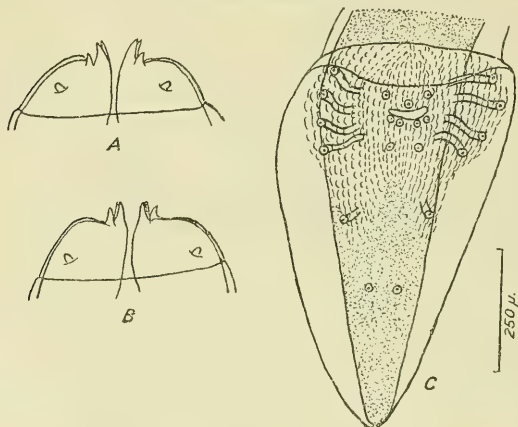
dividing the body into the ratio of 1 : 1.07 to 1 : 1.4. The vagina is straight, and may either pass forwards or backwards; it is muscular, about  $1\frac{1}{4}$  mm. long and  $60\mu$  thick. The egg-chamber may pass forwards with the vagina or be bent backwards; it is about half the length of the vagina, and its breadth varies according to whether it is distended with eggs or not. The common trunk is short, and is nearly  $300\mu$  long; its posterior end divides into two to give rise to the two uteri.

The eggs are thick-shelled and oval, measuring on the average  $41\mu$  long and  $23\mu$  in diameter.

#### *Male.*

The two males are respectively 17 and 18 mm. long, and are .5 mm. thick in their posterior third. The body is much attenuated in its anterior half.

Text-figure 1G.



*Physaloptera alata* Rud.

A & B = Ventral view of lips, showing variations in size of the external tooth.

C = Caudal extremity of male.

The bursa is relatively narrow and lanceolate in shape. There are five pairs of pedunculated lateral papillae, of which two pairs are pre-anal and the rest post-anal in position; the anterior four pairs are equidistant from each other, whereas the distance separating the 4th and 5th pairs is about three times that separating the other pairs; this last pair is also more ventral in origin than the others. There are five pairs and an unpaired ventral papillae; one pair and the unpaired papilla are situated in a triangle in front of the anus, the remaining four pairs being post-anal. The 1st and 2nd post-anal pairs are small, and are found on the posterior margin of the anus; the 3rd pair is situated just behind the level of the 4th pair of stalked papillae;

the 4th pair is at the middle of the tail, and it divides the distance from the last pair of pedunculated papillæ to the tip of the tail in about the ratio of 1 : 2.

The ventral surface of the bursa is ornamented with longitudinal rows of tubercles extending slightly posterior to the last pair of stalked papillæ.

The spicules are short, equal, and pointed; the right, however, has a slightly stouter base; they are  $275\ \mu$  long, the left spicule being 25 and the right  $30\ \mu$  thick at its base.

Hosts: *Falco gallicus*. Intestine. Museum, Vienna; bottle 4439.

*Falco pennatus*. Stomach. Museum, Vienna; bottle 4442.

*Discussion*.—This material differs from Schneider's (1866), von Linstow's (1877), and Seurat's (1914*c*) descriptions of this species in the nature of the teeth and in the arrangement of the male bursal papillæ; these two characters are in keeping with *Ph. subalata* Schn., 1866, and *Ph. galinieri* Seurat, 1914. As the specimens examined consisted of the paratypes of *Ph. alata*, it appears to me that the conception of the species has been erroneous. Further, it would appear that Seurat's species *Ph. galinieri* is either a synonym or a variety of *Ph. alata*, because it agrees with Rudolphi's species in the nature of the teeth, the arrangement of the male bursal papillæ, the very posterior position of the vulva, and the anterior direction of the vagina; it differs from *Ph. alata* in its relatively shorter œsophagus and in its slightly longer and subequal spicules.

Rudolphi described this species from three hosts in the Vienna Museum, viz. *Falco nisus*, *F. pennatus*, and *F. gallicus*. I take his specimens from the first-named host to be the types of this species, and the material from the other two hosts to be the paratypes.

An extracted description of *Ph. galinieri* Seurat is included in Part II.

#### (8) PHYSALOPTERA RETUSA Rudolphi, 1819. (Text-figs. 11 & 12.)

Syn. *Spiroptera retusa* (Rud., 1819), Duj., 1845.

I have been able to examine two lots of material of this species, both having been collected from the Teguexin. The first lot consisted of specimens deposited in the Vienna Museum (bottle 4497), and the second I collected from a Teguexin which died in the Gardens of the London Zoological Society. Both sets of material were in all respects identical.

The cuticle is very finely striated transversely and, in addition, shows a coarse irregular ringing. Anteriorly it is partly or wholly reflected over the lips.

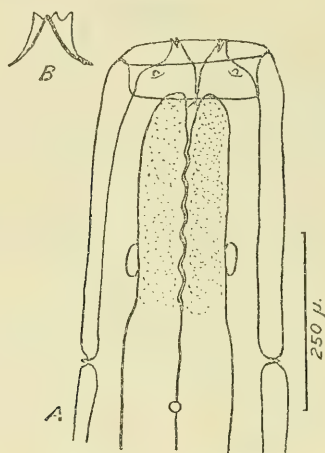
The cervical papillæ are inserted generally symmetrically on either side, but sometimes one may be slightly more anterior to the other; they are lodged a short distance behind the junction

of the two œsophageal parts. The excretory pore is situated about  $50\ \mu$  further back.

The lips are large and somewhat triangular in side view, and each carries on its apex a large triangular tooth. Immediately internal to it there is a slightly larger but membranous tooth, whose free extremity is tripartite. No lateral teeth are present. Each lip bears on its outer surface two conspicuous papillæ.

The œsophagus is long, and in the female it is about  $1/7$ th, in the male slightly more or slightly less than  $1/5$ th of the body-length. Its anterior region is differentiated into a short muscular portion, about  $400\ \mu$  long in fully-grown specimens and slightly thinner than the rest of the œsophagus; the large nerve ring encircles it in its posterior quarter.

Text-figure 11.



*Physaloptera retusa* Rud.

A = Ventral view of cephalic extremity.

B = External aspect of median teeth.

#### *Female.*

The largest female measured 45 mm. long, and 1.2 mm. broad in the middle; fully mature females varied in size from 20 mm. upwards. The body is rather robust, tapering only slightly towards both ends; the tail, however, is sharply set off from the body, and is relatively short and slender; it forms on an average  $1/107$ th of the total body-length, and its caudal pores are situated in its posterior third.

The vulva opens on a level with the general surface, and is situated some distance behind the end of the œsophagus. Its position varies slightly in different individuals, but in general it is seen at the junction of the 1st and 2nd quarters of the body. It leads in the largest females into a relatively short and thick-

walled vagina, about 1.1 mm. long and 100  $\mu$  in diameter. The following egg-chamber is about 3/4ths of the length of the vagina and about twice as broad. The common trunk is very short, so that in some cases it appears to be absent; its posterior end divides into two branches, each of which connects up with one of the two uteri.

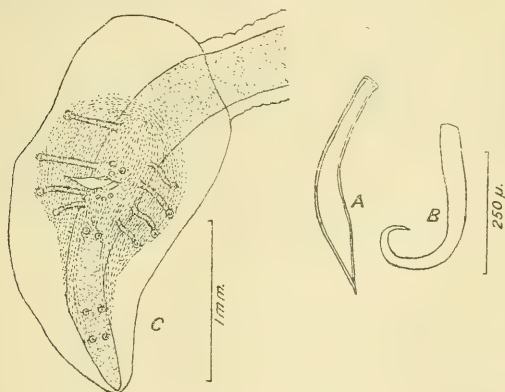
The receptacula seminis are slightly oval, 380  $\mu$  long by 280  $\mu$  broad; they are distinctly constricted off from the oviducts, but their junction with the uteri is very gradual.

The eggs, which on the average are 43  $\mu$  long and 27  $\mu$  in diameter, contain fully-developed embryos *in utero*; they are thick-shelled and oval.

#### Male.

The males are much smaller than the females, the longest measuring 20 mm. long and 570  $\mu$  broad. Anteriorly the body

Text-figure 12.



*Physaloptera retusa* Rud.

A = Left spicule.      B = Right spicule.

C = Caudal extremity of male.

(The scale alongside B refers also to A.)

tapers very gradually, but posteriorly hardly any narrowing takes place until a very short distance in front of the bursa; here the thickness becomes sharply less, so that at the juncture of the bursa it is only about 3/4ths of the thickness further forwards.

The male bursa is large, measuring about 2.3 mm. long by 1.1 mm. broad in the largest specimens, and is sharply reflected ventralwards. The cuticular expansions are well developed, and the four pairs of pedunculated papillæ supporting them are situated equidistant from each other, two pairs being pre-anal and two pairs post-anal. The ventral surface of the bursa is covered by numerous longitudinal rows of small protuberances.

There is one pair and an unpaired median ventral papillæ in front of the anus. These are so placed as to form a triangle with its apex directed towards the anus. Behind the anus there are five pairs of ventral papillæ, of which the first two pairs are situated immediately behind the anus. The third pair is placed at the junction of the 1st and 2nd quarters of the tail, whilst the 4th and 5th pairs are situated further back, and are slightly approximated. Equidistant from these last two pairs there is seen what appears to be a very small papilla, but which probably is the opening of the caudal glands.

The spicules are only very slightly unequal, the right spicule being the longer and more slender. Some difficulty was encountered in making out their lengths in cleared specimens because of their paleness, and consequently they were dissected out by means of a dissecting microscope. The left spicule broadens posteriorly to about  $90\ \mu$  and then gradually tapers to a point; it is  $455\ \mu$  long, and  $32\ \mu$  broad at its base. The right spicule, which is  $475\ \mu$  long, and  $45\ \mu$  broad at its base, tapers gradually to a point, and in all the males examined its posterior extremity was recurved.

Host: *Tupinambis teguixin*. Stomach. Brazil.

In addition to the material described above, I have also examined a few specimens from the mouth of a Hog-nosed Snake (*Heterodon platyrhinus*, S. America) which I have referred to the above species. They agree with *Ph. retusa* in practically all respects except in the size of the spicules, which in this material are equal in length and  $300\ \mu$  long. Their shapes, however, are identical with those described above.

#### (9) PHYSALOPTERA MONODENS Molin, 1860. (Text-figs. 13 & 14.)

The material on which the study of this species is based was collected from *Boa constrictor* and deposited in bottle 4459 in the Vienna Museum.

The cuticle is finely striated and completely reflected over the lips. The cervical papillæ vary in their position, in some cases being at the level of the hind end of the muscular oesophagus, and in others as much as  $300\ \mu$  further back. The excretory pore is situated about  $400\ \mu$  behind the muscular oesophagus.

The lips are dome-shaped, and each bears a small subdorsal and subventral external papilla. The two median teeth are of unequal size, the inner one being much smaller; the outer tooth is sharply conical, the inner foliaceous and tripartite; they are rather small.

The muscular oesophagus forms about  $1/10$ th of the whole organ, which is about  $1/5\cdot3$  of the body-length in the male and  $1/8$ th in the female. The nerve ring encircles its muscular portion in its posterior quarter.



*Female.*

Mature females vary in length from 25 to 40 mm., with a maximum thickness of 850 to 960  $\mu$ ; its greater portion is of more or less uniform thickness, tapering being confined only to the last few millimetres of the two extremities. The tail is obtuse, and forms about 1/75th of the body-length.

The vulva is protuberant, and its position divides the body into the ratio of 1:5. It leads into a slightly coiled vagina 1.6 mm. long by 65  $\mu$  thick. The following egg-chamber is relatively short and thin, being 640  $\mu$  long and 130  $\mu$  in diameter. The common trunk is very short, being only 160  $\mu$  long and as thick as the vagina; its posterior end divides once to give rise to the connections of the two uteri.

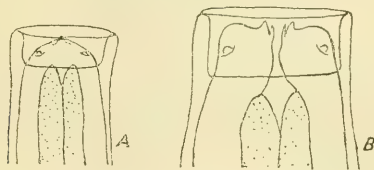
The receptacula seminis are oblong, 240  $\mu$  long and 175  $\mu$  in diameter.

The eggs are thick-shelled, oval, and embryonated *in utero*; they measure 45 by 26  $\mu$ .

*Male.*

In the males the body is attenuated only in its anterior third; the longer specimens varied from 18 to 23 mm. long by 710 to 770  $\mu$  thick.

Text-figure 13.

*Physaloptera monodens* Mol.

A = Cephalic extremity, lateral view.

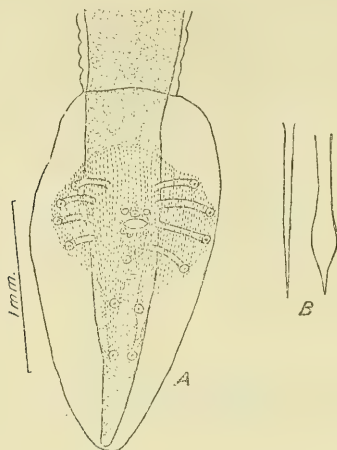
B = Cephalic extremity, ventral view.

The bursa is ovoid, has well-developed alæ, and its ventral surface shows longitudinal rows of small irregularly rounded tubercles. The three anterior pairs of stalked papillæ are pre-anal in position. Of the three pre-anal ventral papillæ the central one is the largest, and is situated closer to anus than the other two. There are five pairs of post-anal ventral papillæ, of which the first two pairs are small and situated in a row immediately behind the anus; the 3rd pair is slightly obliquely placed at about the junction of the 1st and 2nd sixths of the tail; the 4th pair is just in front of the middle of the tail. The distance separating the 4th from the 5th pair is slightly less than that between the 3rd and 4th pairs. The caudal pores

are conspicuous, and are found between the last two pairs of ventral papillæ.

The spicules are unequal, and the left has its end broadened out to form a kind of spear-head; it is  $415\mu$  long and  $38\mu$  broad at

Text-figure 14.



*Physaloptera monodens* Mol.

A = Caudal extremity of male.

B = Right and left spicules.

its base. The right spicule is shorter and thinner, and tapers to a fine point; it is  $362\mu$  long by  $32\mu$  broad at its base.

Host: *Boa constrictor*. Stomach and intestine. South America.

Types in bottle 4459 in the Vienna Museum.

For affinities see *Ph. obtusissima*.

(10) *PHYSALOPTERA OBTUSISSIMA* Molin, 1860. (Text-figure 15.)

The specimens of this species which were examined were deposited in bottles 4463 and 4470 in the Vienna Museum; in both cases the host was simply given as *Colubri*, N. 58.

The cuticle is slightly reflected over the base of the lips, and is provided with a fine transverse striation. The cervical papillæ pierce it from 130 to  $225\mu$  behind the level of the posterior end of the muscular œsophagus, and the excretory pore is situated about  $100\mu$  further back.

The lips are hemispherical in lateral view and slightly flattened. The external tooth is large and bluntly conical, and is slightly bent outwards; the inner tooth is membranous, tripartite, and of the same height as the outer. The two external lip papillæ are large.

The œsophagus is straight and short; in the female it forms

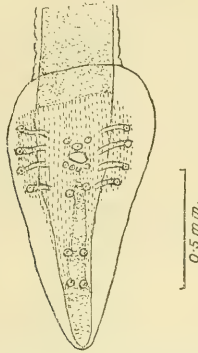
about  $1/9$ th and in the male about  $1/7$ th of the total body-length. Its muscular part is slightly thinner, and the nerve ring is situated in its last quarter.

*Female.*

The females are rather slender, mature worms varying from 28 to 47 mm. long by  $650$  to  $720\ \mu$  thick in their posterior third. The body is much attenuated in its anterior half and in its posterior quarter. The tail is short and bluntly conical, and forms  $1/80$ th of the body-length; its caudal pores are situated behind its middle, and their position divide the tail in the ratio of 3 : 2.

The vulva is situated on a slight elevation at the junction of the 1st and 2nd quarters of the body. It leads into a straight vagina  $1.5$  mm. long by  $65\ \mu$  thick; the following egg-chamber is oblong and  $640\ \mu$  long by  $175\ \mu$  broad; the common trunk is

Text-figure 15.



*Physaloptera obtusissima* Mol.

Caudal extremity of male.

short, and half again as thick as the vagina; it is  $320\ \mu$  long, and its posterior end divides to give rise to two branches, each of which joins up with a uterus. The proximal parts of the uteri may be much convoluted in some individuals; posteriorly each terminates in a receptaculum seminis, which is long and oval, measuring  $400\ \mu$  long by  $160\ \mu$  broad.

The eggs are fully embryonated *in utero*; they are oval and thick-shelled, and measure  $45$  by  $26\ \mu$ .

*Male.*

The males are comparatively stouter than the females; they vary in length from 20 to 32 mm., with a maximum thickness of  $700$  to  $720\ \mu$ . The body is attenuated only in its anterior third.

The caudal bursa is elongate and somewhat lanceolate in shape; its alæ are well developed and its ventral papillæ are

large. The stalked papillæ are equidistant, two pairs being pre-anal and two pairs post-anal. Of the three pre-anal ventral papillæ, the central one is large, and is situated nearer the rim of the anus than the other two. There are four post-anal sessile papillæ, of which the first two pairs are small and arranged in a row immediately behind the anus; the 3rd pair is slightly obliquely placed just behind the level of the last pair of stalked papillæ; the 4th pair is at about the middle, and the last pair at the junction of the 2nd and last thirds of the tail.

The spicules are short and slightly unequal; the right is  $385\ \mu$  long by  $38\ \mu$  broad at its base, and tapers to a fine point; the left is  $430\ \mu$  long by  $38\ \mu$  broad at its base; its posterior half broadens out to about  $74\ \mu$  to form a comparatively large spear-head.

The ventral surface of the tail is traversed by longitudinal rows of irregular tubercles of the same size and shape as those found in *P. monodens*.

Host: *Colubri*, N. 58. Brazil.

This species appears to be closely allied to *Ph. monodens*, with which species it agrees in the arrangement of the caudal papillæ of the male, the general shape of the spicules, markings on the bursa, and size of the eggs. It differs from this species, however, in its larger teeth, more posterior position of the vulval aperture, shorter œsophagus and larger receptacula seminis.

Von Drasche (1883) states that the inner teeth are very small; my observations showed that they were in nearly all cases of the same size as the outer teeth, and could be easily seen from either lateral or ventral (dorsal) views of the lips.

(11) *PHYSALOPTERA BONNEI*, sp. n. (Text-figs. 16 & 17.)

The material consisted of four females and two males, collected from a "Sapakara," Dutch Guiana; the females varied in length from 41 to 50 mm., and the males are respectively 26 and 33 mm. long.

The cuticle is transversely striated, the striæ being about  $\mu 4$  apart. In addition there is a very distinct and coarse ringing. It is only very slightly reflected over the base of the lips.

The cervical papillæ are situated some distance behind the junction of the two œsophageal parts, this distance being about half the length of the muscular œsophagus. The excretory duct opens to the exterior about  $150\ \mu$  further back.

The lips are somewhat flattened, and each has two outer papillæ. Only two teeth are present on each lip, an outer and an inner median tooth. They are of the same size, the outer being conical and obtuse, whereas the inner is membranous and tripartite.

The muscular œsophagus is only slightly thinner than the glandular, and the nerve ring is situated at the junction of its

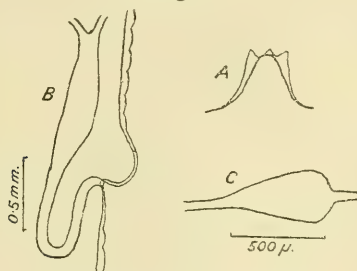
3rd and last quarters. The whole organ forms in the male  $1/5.6$ , in the female  $1/7.6$  of the body-length.

*Female.*

The female is slightly attenuated towards both extremities, and is terminated posteriorly by a slender tail, forming  $1/56$ th part of the body. Its caudal pores are situated at the junction of its 2nd and last thirds. The maximum breadth of the largest female is 1.3 mm. just behind its middle.

The vulva is situated in a depression partly overhung by an anterior cushion-like thickening of the body; it divides the body in the ratio 1 : 2.5. The vagina is coiled, and is 1.2 mm. long by  $95\mu$  thick; the following egg-chamber is about 1 mm. long and twice as broad as the vagina; its posterior end divides into two, and each branch joins up with a uterus, a common trunk being absent. The anterior half of the vagina, the egg-chamber, and the terminal portions of the uteri are directed forwards, the

Text-figure 16.



*Physaloptera bonnei*, sp. n.

A = Outer view of median teeth.

B = Terminal portion of female genitalia.

C = Receptaculum seminis.

uteri extending as far as the base of the œsophagus, when they bend sharply backwards and pass almost to the posterior end of the body. The receptacula seminis are pear-shaped, and are  $480\mu$  long by  $265\mu$  broad at their junction with the oviducts.

The eggs are elongate, oval, and thick-shelled, and contain fully-developed embryos; on the average they are  $42\mu$  long by  $25\mu$  broad.

*Male.*

The males are much thinner than the females, the diameters of the larger and smaller worms being respectively  $950$  and  $850\mu$ . The bursa is large, forming about  $1/14$ th of the body-length, and is nearly twice as long as broad. Ventrally it is ornamented with longitudinal rows of cuticular elevations. The four pairs of pedunculated lateral papillæ are equidistant, two pairs being pre-anal and two pairs post-anal. The three pre-anal papillæ are situated in a row just above the anus. Behind the anus there



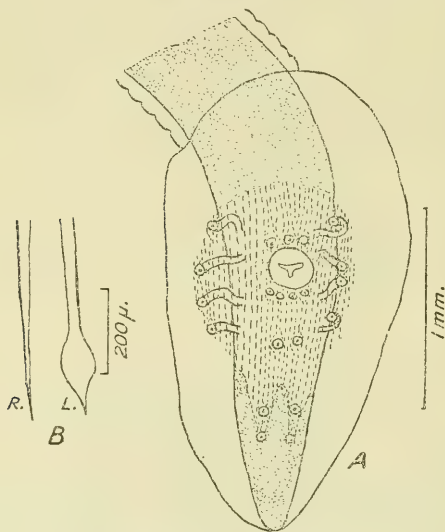
are five pairs of sessile papillæ, of which the first two pairs are small and inserted in a line just behind the anus; the 3rd pair is found at the level of the last part of pedunculated papillæ, the 4th pair in the middle of the tail, and the last just anterior to the front limit of the posterior third of the tail.

The spicules are of equal length, but the base of the right is very slightly thicker than that of the left. They are  $455\mu$  long, the right being  $29\mu$  broad at its base and tapering gradually to a fine point, the left being  $32\mu$  thick as its base and having its posterior end widened out to form a spear-head  $160\mu$  long by  $95\mu$  broad.

Host: "Sapakara." Stomach. Dutch Guiana.

Types in the Helminthological Department of the London School of Tropical Medicine.

Text-figure 17.



*Physaloptera bonnei*, sp. n.

A = Caudal extremity of male. B = Spicules.

This species has many characters in common with *Ph. obtusissima*, as shown by the general shape, ornamentation and arrangement of the papillæ of the male bursa, the nature and size of the teeth, and the general shape of the spicules. It is, however, distinguished from it by its longer oesophagus, slightly more posterior position of the vulva, the presence of a cushion-like swelling anterior to the vulva, the absence of a trunk portion behind the egg-chamber, and in that the spear-head of the left spicule is better set off.

I have named this species after Dr. Bonne, of Surinam, who collected and presented this material to Professor Leiper.

## (12) PHYSALOPTERA PHRYNOSOMA, sp. n. (Text-figure 18.)

Numerous specimens were collected from several lizards which had died in the Gardens of the London Zoological Society; unfortunately only a few of the females are mature.

The parasites are slender and much attenuated anteriorly; their greatest diameter is in their posterior third.

The cuticle is smooth (?), and is not reflected over the lips. The cervical papillæ are situated just in front of the level of the junction of the two œsophageal parts, and the excretory pore from 50 to 100  $\mu$  behind them on the ventral surface.

The two lips are somewhat conical, and each is surmounted by a large conical tooth, which is inclined slightly outwards; no other teeth are present. Each lip has two papillæ on its outer surface.

The œsophagus is straight, and varies in the females from 1/6th to 1/7th, and in the male it is slightly less than 1/5th of the total body-length; its anterior muscular part passes gradually into the following glandular part, there being little difference in the diameters of the two. The nerve ring encircles its anterior part just in front of the junction of its third and last quarters.

*Female.*

Fully mature females vary in length from 18 to 23 mm., with breadth from 610 to 760  $\mu$  in their posterior third. The genital aperture is non-protuberant, and is situated more or less at the junction of the first and second body thirds; its position varies slightly in different individuals, being sometimes slightly in front of or slightly behind this level. It leads into a short and thick-walled vagina, 380  $\mu$  long by 38  $\mu$  in diameter; this in turn leads into a well-developed egg-chamber measuring 950  $\mu$  long by 152  $\mu$  broad; the posterior end of this chamber narrows suddenly and passes into a short common trunk, which after a very short trajet divides into the two uteri; the uteri pass parallel to each other into the posterior sixth of the body.

The eggs are oval and thick-shelled; they measure 50  $\mu$  long by 36  $\mu$  in diameter.

The receptacula seminis are small and oval, measuring 133  $\mu$  by 86  $\mu$ .

The tail is relatively long and slender, forming 1/36th of the total length; its caudal pores are situated just behind its middle.

*Male.*

The males are much slenderer than the females, their average length being 11 mm. by 470  $\mu$  broad. The caudal bursa has well-developed alæ, and its ventral surface is covered with longitudinal rows of small tubercles. Two pairs of the stalked papillæ are pre-anal, and two pairs are post-anal in position; they are more or less equidistant from each other, but the pre-anal pair nearest the anus is slightly more dorsal in origin than the others. There are three ventral pre-anal papillæ, the median unpaired one being situated nearer the anus than the other two. Immediately

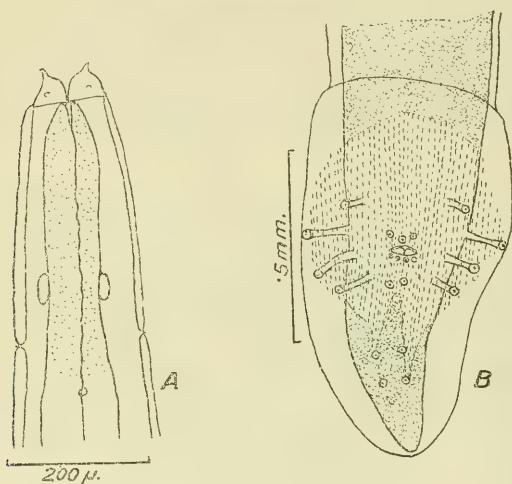
posterior to the anus there are two pairs of small papillæ close together, the one pair being slightly behind the other pair; a small distance behind these there is another pair somewhat obliquely placed and also larger; posterior to the middle of the tail there are two further pairs dividing this part of the tail into thirds.

The spicules are unequal, the right being slightly stouter than the left; both taper to fine points. The right spicule is  $180\mu$  long and  $10\mu$  broad at its base, while the left spicule is  $530\mu$  long and  $9\mu$  broad at its base.

Hosts: *Phrynosoma cornutum*, *P. regale*. Stomach. Brazil.

Types to be deposited in British Museum of Natural History, London.

Text-figure 18.



*Physaloptera phrynosoma*, sp. n.

A = Ventral view of cephalic extremity. B = Caudal extremity of male.

*Affinities.*—*Ph. abbreviata* has been recorded from this host, but it seems doubtful whether the determination was correct; this species was present in nearly every one of the specimens of *Phrynosomæ* examined by me, which numbered about a dozen, and was the only species present; it is therefore possible that it was this species which was mistaken for *Ph. abbreviata*. As redescribed by Seurat (1914*b* and 1917*a*), *Ph. abbreviata* is readily distinguished from *Ph. phrynosoma* by the fact that it has four uteri, whereas the latter has only two.

The presence of two uteri and a single tooth to each lip allies this species to *Ph. gracilis*, sp. n., and to *Ph. longissima*, sp. n.; it is, however, easily separated from these two species by its much shorter and relatively stouter body.

## (13) PHYSALOPTERA GRACILIS, sp. n. (Text-fig. 19.)

The material consisted of about half-a-dozen specimens, all of which were coiled up watch-spring like; as no mature eggs were observed, it is probable that the worms, although fully developed, had not yet reached the reproductive stage.

The cuticle shows a very fine transverse cuticular striation, and it may be partly or wholly reflected over the lips.

The cervical papillæ are situated at the level of the junction of the two œsophageal parts or just posterior to this; the excretory pore is situated on the ventral surface about  $40\mu$  further back.

The lips are simple and triangular in side view, and each is surmounted by a large external tooth, triangular in shape, and having a spike-like internal tooth attached to its inner surface; a row of small denticles is present on either side of it, each row being terminated laterally by two larger denticles. External lip papillæ were not observed.

The œsophagus is slender, and retracted from the lips, so that an elongate chamber is formed between it and the lips. The muscular part is slightly thinner than the following glandular part, and forms in the male  $1/12$ th and in the female  $1/14$ th of the whole organ. The whole œsophagus forms in the male about  $1/7$ th and in the female  $1/6.2$  of the total length of the body. The nerve ring divides the muscular œsophagus in the ratio of 3 : 2.

*Female.*

The females vary in length from 20 to 24 mm., and in breadth from  $240$  to  $250\mu$ ; the body is attenuated towards both extremities, but this is only slightly evident posteriorly. The tail is short and pointed, and forms  $1/97$ th part of the total length.

The vulva is non-protuberant, and leads into a straight vagina  $410\mu$  long by  $45\mu$  broad; the egg-chamber which follows is about as wide again as the vagina, and is  $730\mu$  long; the common trunk has more or less the same dimensions as the vagina; from its posterior end the two uteri take their origin, and these pass down the body more or less parallel to each other. The position of the vulva divides the body into the ratio of 1 : 2.

No mature eggs were observed.

*Male.*

The males average about 19 mm. in length by  $230\mu$  broad; they are more slender than the females, and do not become attenuated towards the posterior end.

The bursa is small, forming  $1/36$ th of the body-length; it is nearly  $2\frac{1}{2}$  times as long as it is broad, and its width is only very slightly greater than the maximum body-breadth. Its ventral surface is free from cuticular protuberances, except for a small area surrounding the anus.

The lateral stalked papillæ are arranged three pairs pre-anal

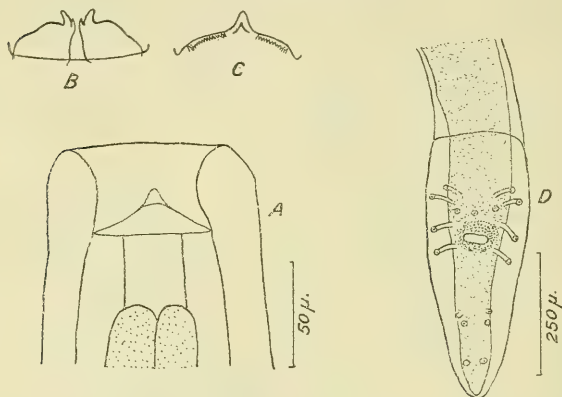
and one pair post-anal; the 1st pair is more ventral in origin than the others, and is also closely approximated to the 2nd pair; the remaining pairs are equidistant from each other. There are three pre-anal and four pairs of post-anal ventral papillæ; the 1st pair of post-anal papillæ are situated immediately behind the anus, the 2nd and 3rd pairs are near together just behind the middle of the tail, and the last pair midway between the 3rd pair and the tip of the tail.

The spicules are unequal, the right being short and stout, measuring  $105\ \mu$  long by  $23\ \mu$  broad, the left being slender, measuring  $273\ \mu$  long by  $7\ \mu$  broad at its base; the right spicule tapers to an obtuse point, whereas that of the left side forms a very fine point.

Host: "Lizard." Uganda.

Types in the Helminthological Department of the London School of Tropical Medicine.

Text-figure 19.



*Physaloptera gracilis*, sp. n.

A = Cephalic extremity, lateral view.

B = Ventral view of lips.

C = Inner view of lip.

D = Caudal extremity of male.

*Discussion.*—The arrangement of the bursal papillæ in the male, the absence of cuticular markings on the greater part of ventral surface of the caudal extremity of the male, and the character of the lips and its teeth—each of these distinguish this species from all the other reptilian didelphoid forms.

There is some similarity in the arrangement of the bursal papillæ of this species to that found in *Ph. leptosoma* (Gervais), Seurat, 1917, except that just behind the anus there are two pairs in this latter species instead of one. *Ph. gracilis*, however, is easily distinguished from this species by the additional characters of a more elongate body and of much shorter spicules.



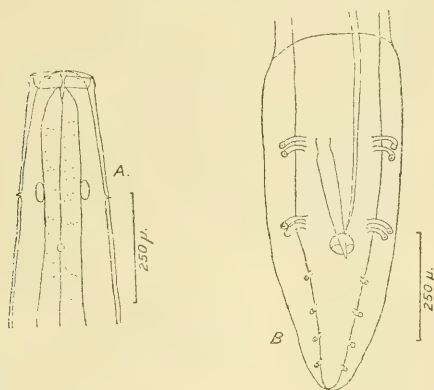
## (14) PHYSALOPTERA LONGISSIMA, sp. n. (Text-fig. 20.)

The material consisted of about two dozen specimens, some of which were still immature. The specimens are remarkable for their slenderness, the largest females having a thickness of less than  $500\mu$ . The body shows very little attenuation towards the extremities.

The cuticle is finely striated transversely, and in some cases it forms a small swelling round the head, whereas in others it is reflected over the lips.

The cervical papillæ and excretory pore occupy a very anterior position, the former being found at the level of the nerve ring, and the latter half-way between the nerve ring and the level of the base of the muscular œsophagus.

Text-figure 20.

*Physaloptera longissima*, sp. n.

A = Ventral view of cephalic extremity.

B = Caudal extremity of male.

The lips are rounded, and each carries only a single tooth, namely the external median; this tooth is triangular in shape, and has its tip slightly recurved outwards. Each lip carries two outer papillæ.

There is no difference in diameter in the two œsophageal parts, the two merging gradually into each other; the whole organ attains  $1/7.6$  in the female and  $1/6.6$  in the male of the body-length; the muscular part, which is encircled in its middle by the nerve ring, forms nearly  $1/8$ th of the whole organ.

*Female.*

The largest females are 30 mm. long by  $438\mu$  broad, and possess a vulva which is situated just in front of the middle of

the body, dividing it in the ratio of 7 : 8 ; it leads into a straight vagina 1.3 mm. long, which is directed posteriorly ; it then turns forwards to join the trunk, which in its middle bends back again ; it is 3.5 mm., long and its anterior half is only slightly differentiated into an egg-chamber ; the posterior end of the common trunk divides to give rise to the two uteri. The uteri pass posteriorly almost to the hind end of the body, then pass forwards before joining the oviducts and ovaries, which in their turn pass backwards again.

The body is terminated by a short and rounded tail forming nearly 1/190th part of the body-length.

The eggs are long, oval, and thick-shelled, measuring 59  $\mu$  long, 32  $\mu$  broad, the thickness of the shell being 5  $\mu$ .

#### *Male.*

The males average about 22 mm. long by 325  $\mu$  broad in their middle.

The bursa is not sharply set off from the body, and is only slightly broader than it ; it forms about 1/28th of the body-length ; it is little more than twice as long as it is broad, and its ventral surface is devoid of cuticular markings.

The four pairs of stalked papillæ are all pre-anal in position, and arranged in two widely-separated groups of two pairs each. No ventral pre-anal papillæ were seen. Behind the anus there are four pairs of shortly stalked papillæ, which are equidistant from each other and from the anus. They are situated somewhat laterally.

The spicules are unequal, the left being nearly twice as long as the right ; the left spicule is slender, and tapers to a fine point ; it is 546  $\mu$  long by 22  $\mu$  broad at its base ; the right spicule is from 228 to 300  $\mu$  long by 32  $\mu$  broad at its base ; near its base it has a distinct neck, after which it widens out and then tapers to an obtuse point.

Host : "Snakes." Australia.

Types in the Helminthological Department of the London School of Tropical Medicine.

*Discussion.*—This species is easily separated from all the didelphoid Physaloptera (1) by the arrangement of the stalked bursal papillæ, these being entirely pre-anal and arranged in two widely-separated groups in this species ; (2) by the arrangement and number of the post-anal ventral papillæ ; and (3) by the entire absence of cuticular markings on the ventral surface of the tail of the male.

The elongate and slender body shows some similarity to *Ph. gracilis*, sp. n., from which species it is, however, quite distinct, as shown by the above-named three characters ; it also differs from this species by the difference in shape of its lips and teeth, by the more posterior position of its vulva, and by its larger spicules.

(15) *PHYSALOPTERA PRÆPUTIALIS* von Linstow, 1889. (Text-figs. 21 & 22.)

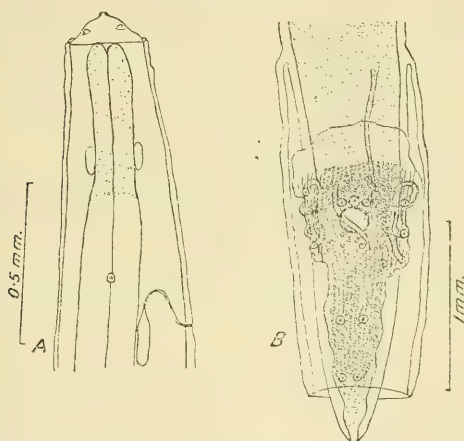
Syn. *Chlamydonema felineus* Hegt, 1910.

Several lots of material were examined, mostly from cats.

The body is slightly attenuated anteriorly, and is surrounded posteriorly by a very loose cuticle, which is partly or wholly reflected over the tail region. The cuticle shows a very fine transverse cuticular striation, and is only slightly reflected over the lips.

The excretory pore and cervical papillæ are situated relatively far back, the former being more posterior in position than the latter. The distance from the anterior end to the cervical

Text-figure 21.



*Physaloptera præputialis* v. Linst.

A = Lateral view of cephalic extremity.

B = Caudal extremity of male.

papillæ in a male 15 mm. long is  $875\ \mu$  and the excretory pore  $990\ \mu$ ; in a female 17 mm. long these distances were  $952\ \mu$  and  $1123\ \mu$  respectively.

The lips are large and conical, and each carries a subdorsal and subventral external papilla. The external median tooth is large and bluntly triangular; the inner median tooth is of the same height as the outer, and is flattened and tripartite.

The œsophagus is long, and varies in the female from  $1/4.8$  to  $1/5.4$  of the body-length; in the male it forms about  $1/4.5$  of the body-length. The muscular portion of the œsophagus is slightly thinner than the glandular, and is encircled by the nerve ring at the junction of its second and last thirds. It forms about  $1/8$ th of the whole œsophagus.

*Female.*

The females are generally large, and vary in length from 15 to 48 mm. with a maximum thickness of 1 to 1.7 mm. in their posterior half.

The vulva opens a short distance in front of the middle of the body. It is non-protuberant, and its position divides the body into the ratio of 1:1.4 to 1:1.1. It leads into a thick-walled, straight or bent vagina 1.6 mm. long by  $114\ \mu$  thick in a female 20 mm. long; its posterior part gradually passes into the egg-chamber, which broadens out posteriorly so as to assume a more or less pyriform shape: in the same female it was  $820\ \mu$  long by  $228\ \mu$  thick at its posterior end. Two uteri take their origin from the posterior margin of the egg-chamber, a trunk portion being entirely unrepresented. The mode of origin of the uteri is very characteristic, and differs from all those already described; they arise from the posterior lateral margins of the egg-chamber, and not from its base. It thus happens that the uteri, although arising at the same level, are yet far removed from each other.

In most individuals a dark and detachable chitinous ring surrounds the body in the region of the vulva.

The tail is conical and rounded at its tip, and forms from 1/53rd to 1/66th part of the body-length. Its caudal pores open in its posterior half, and their position divides the tail into the ratio of 3:1.

The eggs are oval and thick-shelled, and contain a fully-developed embryo; they average  $49\ \mu$  long by  $35\ \mu$  in diameter.

*Male.*

The length of the males varies from 13 to 40 mm. by .7 to 1.3 mm. thick in their posterior third.

The tail is elongate, and is often closely reflexed on to the ventral surface. Its median ventral surface is ornamented with conspicuous and rounded tubercles arranged longitudinally; toward the lateral margins of the tail and on to the alæ these tubercles become gradually replaced by longitudinal ridges, each having a few relatively far removed breaks along its course.

The caudal region, within the cuticular reduplication, appears pointed; this is due to the fact that the caudal alæ, although present, do not open out laterally, but remain irregularly folded towards the ventral surface of the tail. The four pairs of stalked papillæ are thick and equidistant from each other, two pairs being pre-anal and two pairs post-anal. The three pre-anal ventral papillæ are in a transverse row, and the median one is much larger than the other two. Just behind the anus, one pair immediately following the other, there are three pairs of ventral papillæ. Two additional pairs of ventral papillæ are found further down the tail, and their positions divide the tail roughly into thirds.

The spicules are unequal, pointed, and generally curved. The left spicule appears to vary in length from 1 to 1.2 mm., with a thickness of  $32\ \mu$  at its base. The right spicule is slightly stouter than the left; its length also appears to vary from 840 to  $900\ \mu$  with a thickness of  $38\ \mu$  at its base.

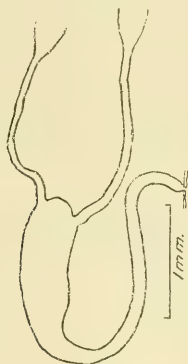
Hosts: *Felis catus domesticus*. Stomach. Federated Malay States, British and Dutch Guiana, China and Ceylon.

*Felis nebulosa*. India.

*Felis pardus*. Stomach. Nigeria.

Although my observations as regards the arrangement of the caudal papillæ in the male, the position of the vulva in the female, and the size of the eggs differ considerably from those of von Listow, yet I am quite satisfied that my material belongs to the same species.

Text-figure 22.



*Physaloptera præputialis* v. Linst.

Terminal portions of female genitalia.

The prepuce-like fold of the cuticle over the tail, the rounded wart-like tubercles on the ventral surface of the tail of the male, the nature of the teeth, the presence of a ring round the body in the vulval region of the female, and the fact that his material is described from *Felis catus*, easily counterbalances the differences in the arrangement of the bursal papillæ. Von Linstow states that this arrangement may be found to be different, as he had only one male for examination, and this specimen he found difficult to study. The ventral papillæ, according to von Linstow, are three pre-anal, one pair immediately behind the anus, three papillæ towards the tail end, and an additional pair slightly in front of these three. He gives the average length of the female as 30 mm., with the vulva 8 mm. from the cephalic extremity and the eggs as  $55$  by  $33\ \mu$ .



## (16) PHYSALOPTERA MALAYENSIS, sp. n. (Text-fig. 23.)

In external appearance this species appears to be identical with *Ph. præputialis* v. L., with which species it was at first confused. This applies especially to the female, where there is a corresponding similarity in the genitalia.

The cuticle is very slightly reflected over the base of the lips, and in most cases the lips are quite naked. The cervical papillæ are situated about  $130\ \mu$  behind the level of the hind end of the muscular œsophagus, and the excretory pore is found about  $100\ \mu$  further back.

The lips are rounded, and each bears a large triangular and slightly recurved outer tooth, internal to which is the foliaceous and tripartite inner tooth of equal height.

The œsophagus forms  $1/5$ th in the male and  $1/6$ th in the female of the total length; its anterior muscular part, which is encircled in its posterior third by the nerve ring, is slightly thinner than the following part, and forms nearly  $1/10$ th in the female and  $1/7$ th in the male of the total organ.

*Female.*

Mature females vary in length from 29 to 38 mm., with breadth of from 1.6 to 2.1 mm. The body is attenuated in its anterior third, but posteriorly, because of the looseness of the cuticle and its reflection over the tail, there appears to be only a very slight thinning.

The vulva opens on a slight bulging, and is situated far back, just in front of the middle of the body; its position divides the body in the ratio of 1:1.2 to 1:1.5. Externally the position of the vulva is indicated by a dark chitinous and detachable band encircling the body. The vulva leads into a vagina, which progressively thickens posteriorly to join a progressively thickening egg-chamber; at its vulvular end the vagina is  $100\ \mu$  thick, at its posterior end it is  $200\ \mu$  thick, and the hind end of the egg-chamber is  $330\ \mu$  in diameter; the whole organ is straight, and measures about 3.3 mm. long. From the basal end of this organ the two uteri take their origin like two horns in the same manner as in *Ph. præputialis*.

The eggs are small, thick-shelled, and only slightly ovoid; they are  $35\ \mu$  long by 28 to  $32\ \mu$  broad.

*Male.*

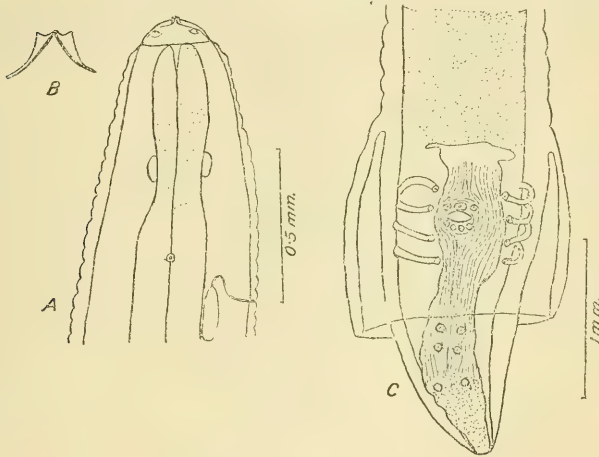
The males are attenuated in their anterior half, and have in most cases the cuticle completely reflected over the tail end; they average in length from 18 to 21 mm., with a maximum breadth of 0.9 to 1.2 mm.

In consequence of the cuticle being reflected over the tail, the bursal expansions are irregularly folded over the ventral surface; they are supported by the usual four pairs of circumcloacal stalked papillæ. The whole of the ventral surface is traversed by well-marked and unbroken longitudinal ridges running more or less parallel to each other. The three pre-anal ventral papillæ

are arranged in a row, and the central one is the largest. There are five pairs of ventral post-anal papillæ; pairs 1 and 2 are small, and arranged in a line immediately behind the anus. The 3rd and 4th pairs are approximated to each other just behind the middle of the tail, and the last pair is at about the junction of the second and last thirds of the tail.

The spicules are unequal, that of the left side being about  $2\frac{1}{2}$  times as long as that of the right side; their lengths appear to vary in different individuals, but this may probably be due to the fact that the spicules do not lie straight in the body, but often have a wavy course; it is thus difficult to measure them accurately; in this way the left spicule was found to vary from 1.4 to 2.5 mm. in length, with a thickness of  $32\mu$  at its base;

Text-figure 23.



*Physaloptera malayensis*, sp. n.

A = Lateral view of cephalic extremity.      B = Outer view of median teeth.  
C = Caudal extremity of male.

the right spicule is slightly stouter, and varies in length from  $580$  to  $957\mu$ , with a breadth of  $36\mu$  at its base. Although there is this marked variation in the sizes, yet it is worthy of note that the ratio of the two spicules was nearly the same in all cases. Unfortunately there was not sufficient material to allow for the dissecting out of the spicules in a series, in order to determine whether this variation was only apparent or real.

Hosts: *Felis chaus*. Intestine. Federated Malay States.  
*Felis tigris*. Stomach. Federated Malay States.  
 "Tiger cat." " Federated Malay States.  
 "Bush cat." " Nigeria.  
 "Hyena." Prob. *H. striata*. Stomach. Nigeria.

Types in the Helminthological Department of the London School of Tropical Medicine.

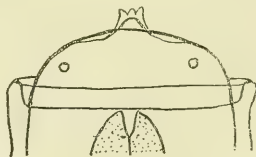
*Affinities.*—This species, because of its labial armature and female genitalia, forms a distinct group with *Ph. præputialis* and *Ph. acuticauda*; to the former it is very closely related, as shown by the similarity of the females and the characteristic reflection of the cuticle over the caudal end in both species; it differs from it, however, by the arrangement of its post-anal ventral papillæ, its larger spicules, and by the presence of unbroken ridges on the ventral surface of the bursa.

The arrangement of the papillæ on the caudal extremity of the male is very similar to that found in *Ph. terdentata*. Apart from this characteristic, and that these two species are both parasitic in carnivores, there appears to be no close affinity between them. *Ph. malayensis* differs from *Ph. terdentata* by the shape and size of its teeth, length of its spicules, presence of unbroken ridges on the male bursa, and in that the cuticle is reflected over the caudal extremity.

(17) *PHYSALOPTERA TERDENTATA* Molin, 1860. (Text-figs. 24 & 25.)

Three bottles of material, Y 1074 from *Felis concolor*, 4511 from *Felis tigrina*, and 4513 from *Felis* sp., labelled *Ph. terdentata* and deposited in the Vienna Museum, were examined. Bottle Y 1074 contained two males, one of which had its head missing. Bottle 4511 contained one female, and bottle 4513 contained one male. The male in the last-named bottle proved to be not *Ph. terdentata* but *Ph. præputialis* v. Linst. The

Text-figure 24.



*Physaloptera terdentata* Mol.

Outer view of lip.

female from bottle 4511 had all the characters of the female of *Ph. præputialis*, except that the cuticle was not reflected over the caudal end, and consequently I am inclined to think that it also is *Ph. præputialis*. The material from *Felis concolor* proved to be *Ph. terdentata*, and the following description of the male is based on these two specimens.

The complete male is 14 mm. long, and 400  $\mu$  thick in its posterior third. The body is attenuated anteriorly, and the cuticle is slightly reflected over the lips; externally it shows a coarse annulation, between which a fine transverse striation is

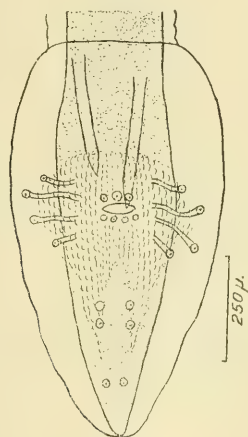
visible under high magnification. The cervical papillæ are lodged about  $100\mu$  behind the posterior limit of the muscular œsophagus, and the excretory pore is situated slightly posterior to them.

The lips are large and flatly rounded, and each carries two large and spherical outer papillæ—one in the subdorsal and one in the subventral line. The two terminal teeth are well-defined, the outer being short and stumpy, the inner large and tripartite.

The œsophagus is straight, and consists of the usual two parts; it is  $2.3\text{ mm.}$  long or about  $1/6\text{th}$  of the total body-length. Its anterior glandular part is slightly thinner than the part following, is  $240\mu$  long, and has the nerve ring situated in its posterior quarter.

The bursa is elongate with rounded tip, and forms nearly

Text-figure 25.



*Physaloptera terdentata* Mol.

Caudal extremity of male.

$1/15\text{th}$  of the body-length. Its lateral alæ are supported by four pairs of equidistant and somewhat slender stalked papillæ, and are arranged two pairs pre-anal and two pairs post-anal in position. Its ventral surface has longitudinal rows of irregular cuticular bosses. The pre-anal ventral papillæ are situated close together in a row just above the anus, and the middle one is slightly larger than the other two. The post-anal ventral papillæ consist of five pairs, of which pairs 1 and 2 are small and arranged in a row just posterior to the anus, pairs 3 and 4 are situated close behind each other in about the middle of the tail, and pair 5 is found at the junction of third and last quarters of the tail.

The spicules are only slightly subequal, the left being  $320\mu$

and the right  $305\mu$  long; they are of equal thickness,  $32\mu$ , and they possess a more or less uniform thickness in their anterior four-fifths, the last fifth tapering to a sharp point.

*Female.*

The female from *Felis tigrina* is 47 mm. long; teeth both large and of equal size, the outer triangular; œsophagus  $1/7\cdot3$  of body-length, vulva situated 18·5 mm. from anterior end, the female genitalia as for *Ph. præputialis*, and the cuticle is not reflected over the tail.

Host: *Felis concolor*. Stomach. Brazil.

Type males in bottle 1074 (number on stopper) in the Vienna Museum.

With regard to the name of the host, the legend on the bottle was somewhat indistinct and appeared somewhat like *Felis casiolaris*, but as no feline of this name is known, I take it to mean *Felis concoloris*.

I have placed this species among the didelphoid forms, because the female described may belong to this species, in which case it would come into the group characterised by *Ph. præputialis* v. Linst.

(18) PHYSALOPTERA ACUTICAUDA Molin, 1860. (Text-fig. 26.)

The material on which the study of this species is based is the type material deposited in the Vienna Museum. This material has also been studied by von Drasche. All the specimens were in an excellent state of preservation.

The cuticle is very finely striated transversely, and anteriorly is partly reflected over the lips. In each lateral line, just behind the level of the posterior end of the muscular œsophagus, a small and spike-like cervical papilla is situated, and on the ventral surface about  $100\mu$  further back is the opening of the excretory organ.

The lips are somewhat rounded in lateral view, and each carries only two teeth, a large and triangular outer tooth, and immediately internal to it a smaller membranous tooth having its free end tripartite. In the subdorsal and subventral lines of each lip there is a conical papilla.

The œsophagus, which immediately follows the lips, has its anterior muscular part slightly thinner than the following glandular portion: in the male it forms about  $1/5\cdot1$  of the total body-length and in the female about  $1/7$ th. The glandular part forms about  $1/7$ th of the œsophagus, and is surrounded by the nerve ring at the level of its posterior quarter.

*Female.*

The females have a length of about 30 mm., with a maximum breadth of just over 1 mm. The body tapers in its anterior half, but posteriorly it narrows only in the vicinity of the tail, which is a conical structure about  $1/56$ th of the total body-length, and has its caudal pores situated in its posterior third.



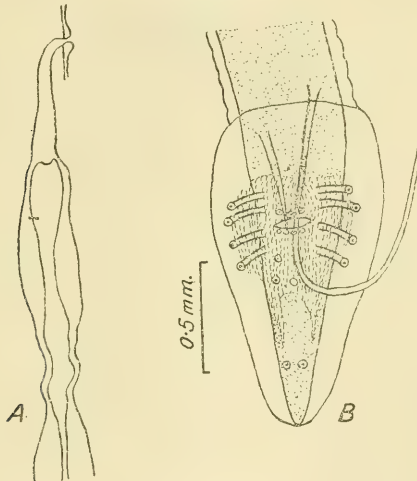
The vulva is situated very far forwards, opening to the exterior on a slight elevation in front of the hind end of the œsophagus. The muscular vagina is very short, measuring only about  $480\ \mu$  long by  $50\ \mu$  broad; its hind end is very slightly enlarged, and from its outer sides the two uteri take their origin in the same manner as in *Ph. præputialis* v. Linst.; the thin initial portions of the uteri are swollen in their middles, after which they again become thin and also much convoluted, after which they join up with the much thicker and egg-containing part of the uteri.

The eggs are large, oval, and thick-shelled, measuring  $51\ \mu$  long by  $42\ \mu$  broad; they are fully embryonated *in utero*.

#### Male.

The males are much smaller and slenderer than the females, measuring only 18 to 23 mm. long by  $620$  to  $740\ \mu$  thick in

Text-figure 26.



*Physaloptera acuticauda* Mol.

A = Terminal portions of female genitalia.

B = Caudal extremity of male.

their posterior third. From about the posterior third the body tapers gradually towards the anterior end.

The caudal bursa has well-developed lateral wings supported by four equidistant, pedunculated and paired papillæ, two pre- and two post-anal. Of the three pre-anal ventral papillæ the median one is lodged nearer the anus than the other two, and is also larger. There are five pairs of ventral post-anal papillæ, of which the 1st and 2nd pairs are situated in a row immediately behind the anus. The distance between the 4th and last pairs is about twice the distance between the 2nd and 3rd pairs.

The spicules are unequal, tubular, and end in sharp points; that of the left side measures 1.89 to 2.17 mm. long by  $45\ \mu$  broad at its base, that of the right 420 to 490  $\mu$  long by  $50\ \mu$  broad.

Host: *Falco cachinnans*. Oesophagus and stomach. Brazil.

Type material in bottle 4431 in the Vienna Museum.

This species occupies an isolated position among the Physaloptera recorded from birds; none of these in which the nature of female genitalia is known have the uteri arising from the margin of the egg-chamber in a way similar to that seen in *Ph. acuticauda*. This peculiarity of the female genitalia allies *Ph. acuticauda* to *Ph. præputialis* v. Linst. and to *Ph. malayensis*, sp. n., from which species it is, however, very easily distinguished by the very anterior position of its vulva, different arrangement of the male caudal papillæ, and difference of the ornamentations on the ventral surface of the male tail.

### GROUP Tetradelphys.

#### (19) PHYSALOPTERA MORDENS Leiper, 1908. (Text-figs. 27 & 28.)

For the study of this species, Prof. Leiper kindly placed at my disposal the type males (three specimens) and also two lots of worms collected by Drs. Turner from man in Africa. In addition, six tubes of worms collected by Dr. Davy from African monkeys were also placed at my disposal for comparison and identification; all these proved to be the same species as that collected from man.

The cuticle shows a very delicate transverse striation; in some specimens an additional coarse and irregular ringing, probably due to a certain amount of shrinkage, is present. It is partly reflexed over the lips in some, whereas in others it stops short at the base of the lips. It is somewhat inflated, so that the cervical papillæ appear to be lodged in shallow cuticular pits. The cervical papillæ are situated slightly less than three-quarters of the length of the muscular oesophagus behind the posterior limit of this oesophageal part. The excretory pore opens ventrally from 50 to 100  $\mu$  further back.

The two lateral lips are large and rounded in lateral view, and are sharply set off from the body in those worms where the cuticle is not reflected over their bases. Each lip carries a large dome-shaped external papilla on each submedian line. Four teeth are present on each lip, one outer and three inner; the outer tooth is large and triangular, and has its tip slightly rounded and recurved outwards. The median inner tooth is very small, and is attached to the base of the outer tooth; it is in the form of a small spike. Leiper states that its inner surface is modified to form a cutting-edge; to me this surface appeared quite flat, or at most slightly convex inwardly. The two inner lateral teeth are situated in the submedian lines, and are directed inwards; each is split longitudinally to its base, and is lodged in a slight elevation of the lip.

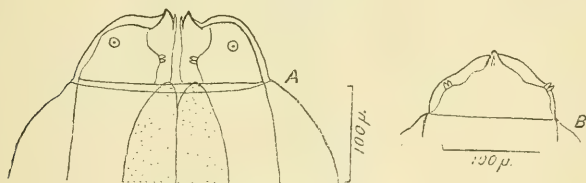
The œsophagus is straight and immediately follows the lips; it thickens very slightly towards the posterior end. Its anterior 1/10th, which is slightly thinner than the rest, forms its glandular part, and the nerve ring encircles it in its posterior third. The entire organ forms 1/6.4 in the male, and 1/6.2 in the female, of the total body-length.

#### *Female.*

The females are large and stout; they vary in length from 41 to 100 mm., with a thickness of 1.8 to 2.8 mm. in their posterior third. The anterior two-thirds taper gradually towards the cephalic extremity; the posterior 1/8th tapers to end in a short and conical tail 1/70th to 1/90th of the body-length; the caudal pores are situated in its posterior half.

The vulva is situated on a slight elevation behind the hind end of the œsophagus; its position divides the body into the ratio of 1:5. The general characters of the female genitalia are exactly similar to those described for *Ph. varani*, except that the common trunk portion behind the egg-chamber is relatively

Text-figure 27.



*Physaloptera mordens* Leiper.

A = Ventral view of lips.

B = Inner view of lip.

larger. The four uteri are twisted about each other in a complicated way, or fill practically the whole of the body as far as its posterior eighth.

The eggs are oval and thick-shelled, and vary from 45 to 49  $\mu$  long by 32 to 34  $\mu$  broad. They are fully embryonated when laid.

#### *Male.*

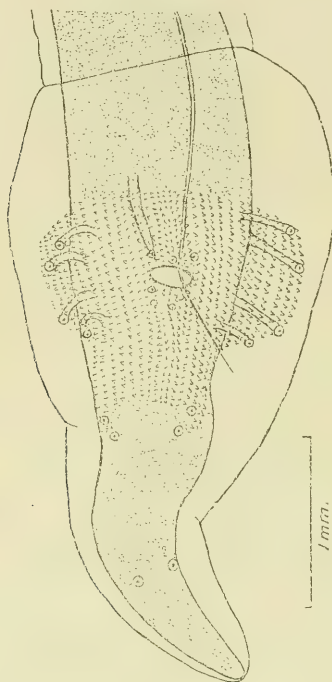
The males vary in length from 29 to 34 mm., with a thickness of .9 to 1 mm. in their posterior quarter; the body is slightly attenuated anteriorly.

The bursa is long and pointed, and is reflexed ventralwards. Its under surface is ornamented with small triangular spike-like processes arranged longitudinally, and extending as far as the 4th pair of post-anal ventral papillæ. The four pairs of stalked papillæ are arranged in two groups, the anterior two pairs being pre-anal and the posterior two pairs post-anal in position; the 1st and last pairs are shorter than the other two, and their origins are slightly more ventral.

The three pre-anal ventral papillæ are of equal size, and are

slightly separated from each other, the middle one being nearer the anus. The first two pairs of post-anal ventral papillæ are small, and are situated close together, one pair behind the other, in the immediate vicinity of the anus; pairs 3 and 4 are approximated to each other, and are situated at the junction of the 1st and 2nd tail thirds; the 4th pair is situated nearer the ventral mid-line than the 3rd pair. The last pair is found at the junction of the posterior tail thirds.

Text-figure 28.

*Physaloptera mordens* Leiper.

Caudal extremity of male.

The spicules are very unequal, the left being long and slender and about eleven times as long as the right; it is filiform, tapers to an acute point, and appears to vary in length from 4.6 to 5.5 mm., with a breadth of 35  $\mu$ . The right spicule is short and stout, with its apex tapering to form a long and thin point; it is 470 to 500  $\mu$  long by 50 to 55  $\mu$  broad at its base.

Hosts: *Homo sapiens*. Stomach and intestine. Africa.

"Monkeys." Stomach. Nyasaland.

My observations differ from Leiper's description, firstly, in the number of uteri, of which he records only two; I was able to

determine their number by dissection, as it is almost impossible to see them by simply clearing and rolling the worms. Secondly, in the size of the females; his longest specimens were 55 mm. long, whereas mine reached 100 mm. And, thirdly, in the size of the spicules; the left spicule, according to my observations, appears to be longer than in his.

The only other *Physaloptera* from man is *Ph. caucasica* v. Linst., 1902. The arrangement of its male bursal papillæ is very similar to that of *Ph. mordens*, except, as Leiper has pointed out, that the 3rd pair of post-anal ventral papillæ is nearer to the mid-line than in *Ph. mordens*. These two species, however, appear to be distinct, as shown by the presence of only one tooth, smaller spicules, and larger eggs, in conjunction with the much smaller body in *Ph. caucasica*.

The nature of the labial armature, mode of origin and number of the uteri, general shape and size of the male bursa, distribution of the bursal papillæ, and the great inequality in the length of the spicules, allies this species to the reptilian species *Ph. abbreviata*, *Ph. varani*, and *Ph. antarctica*. To the mammalian species *Ph. numidica* it is also related, as shown by the number and shape of its teeth and the character of its female genitalia. *Ph. mordens* is, however, easily distinguished from all these by its much larger size, relatively longer trunk portion in the female genitalia, and by its much larger spicules.

The occurrence of this species in monkeys from Nyasaland is very interesting, and leads one to think that these Primates are its normal hosts, man being only an accidental one; this view is further supported by the fact that its only occurrence in man is in the natives of East and Central Africa.

A parallel case in West Africa is the occurrence in monkeys and man of *Esophagostomum apiostomum* (Willach, 1891), Raill. & Henry, 1905.

(20) *PHYSALOPTERA TUMEFACIENS* Henry & Blanc, 1912.  
(Text-figs. 29 & 30.)

The material examined consisted of three males and three females, kindly placed at my disposal by Prof. Leiper. This material was part of the collection of worms from which Henry and Blanc described the species, and was presented to Prof. Leiper prior to the publication of their description. In addition, two males, obtained from a *Macacus fascicularis* which had died in the Gardens of the Zoological Society of London, were also studied.

The cuticle is very finely striated transversely, and also shows a coarse cuticular ring. Anteriorly it is reflected over the lips, and this may also be the case over the tail region in both sexes; this posterior reduplication of the cuticle may pass over as much as the anterior third of the bursa in the male; in the females it only forms a narrow collar in front of the anus. The

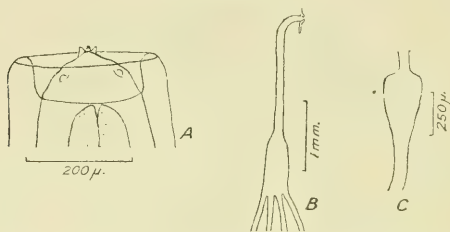


cervical papillæ vary in position; in one they are placed at the junction of the two œsophageal parts, in the others up to  $150\mu$  further back; they may be symmetrical or asymmetrical in position. The excretory pore is found about  $70\mu$  behind the cervical papillæ.

The two lateral lips are large and conical in side view, and each carries two large submedian papillæ on their outer convex surface. Only two teeth are present—a large and conical outer tooth with obtuse tip and slightly bent outwards, and a flattened and broad inner tooth, of the same size as the outer, and having its free end divided into three cusps of the same size.

The œsophagus is straight, and forms in the female  $1/5.2$  to  $1/5.4$ , in the male  $1/4.6$  to  $1/5.2$  of the total body-length; its anterior  $1/11$ th or  $1/12$ th forms its muscular part, which is slightly thinner than its posterior glandular portion. The nerve ring encircles it in its posterior third.

Text-figure 29.



*Physaloptera tumefaciens* Henry & Blanc.

A = Lateral view of lips.    B = Terminal portions of female genitalia.  
C = Receptaculum seminis.

*Female.*

The three females are 50, 38, and 36 mm. long, with a thickness of respectively 1.9, 1.5, and 1.2 mm. The anterior half tapers considerably, but posteriorly this tapering is limited to the last 4 or 5 mm. The tail is conical, and forms from  $1/57$ th to  $1/65$ th part of the body. Its caudal pores are situated in slight pits in the posterior half of the tail; their position divides the tail into the ratio of 5 : 2.

The vulva opens on a slight elevation, which divides the body into the ratio of 1 : 2.9; in one of the females it is situated in front of the end of the œsophagus; this position is probably due to shrinkage of the anterior part of the worm, as shown by the facts that the cuticle in this region is much corrugated and that the intestine immediately behind the œsophagus is thrown into a loop.

The genitalia pass straight back, and are specially characterized by the absence of a common trunk portion behind the egg-chamber, and by the presence of four uteri arising all together from the hind end of the egg-chamber. The vagina, in the

largest female, is 1.7 mm. long by  $100\mu$  thick, and the egg-chamber  $800\mu$  long by  $270\mu$  broad at the origin of the uteri. The receptacula seminis are pear-shaped, and are sharply constricted off from the oviducts, their union with the uteri being gradual; they are  $380\mu$  long by  $200\mu$  broad at their oviducal end.

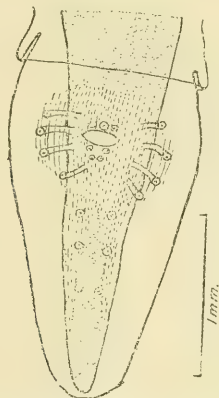
The eggs are oval and thick-shelled, and average  $43\mu$  long by  $27\mu$  thick. They contain a fully-developed embryo when laid.

#### *Male.*

The males vary in length from 26 to 31 mm., and are attenuated in their anterior two-thirds; they vary in thickness from 1 to 1.2 mm.

The bursa is narrow and elongate and rounded at its tip; its anterior part may or may not be covered over by a posterior

Text-figure 30.



*Physaloptera tumefaciens* Henry & Blanc.

Caudal extremity of male.

reflection of the cuticle. Its central ventral area is ornamented with irregular tubercles arranged longitudinally; laterally in the cloacal region these tubercles are replaced by longitudinal ridges.

The four stalked papillæ are short and arranged equidistant from each other round the cloaca. The three pre-anal ventral papillæ are situated in a row just anterior to the anus; the central papilla is large. There are five pairs of post-anal ventral papillæ, of which the first two pairs are small and situated close together, one behind the other, immediately posterior to the anus. Papilla 3 are situated at the anterior quarter of the tail, and papillæ 4 half-way between them and the middle of the tail. Papillæ 5 are slightly approximated to the mid-line, and are situated slightly behind the middle of the tail.

The spicules are bent, thick, short, and slightly unequal.

They are of equal thickness, and both taper to fine points. The right varies from 475 to 520  $\mu$  long by 55  $\mu$  thick, and the left from 740 to 870  $\mu$  long, with the same thickness as the right.

Hosts: *Macacus cynomolgus*. } Stomach. India.  
*Macacus fascicularis*. }

My observations on this species are practically identical with those of Henry and Blanc; the only differences are in the size of the egg, which appears slightly smaller in my material, and in the size of the spicules, mine being slightly larger.

*Ph. tumefaciens*, *Ph. mordens*, *Ph. numidica*, and *Ph. magnipapilla* are the only 4-uterine forms described from mammals. *Ph. mordens* and *Ph. numidica* have teeth as in *Ph. paradoxa*, whereas *Ph. magnipapilla* and *Ph. tumefaciens* have each only two teeth to each lip. *Ph. tumefaciens* is distinguished from the other three species by the mode of origin of its uteri, by the absence of a common trunk portion in the female genitalia, and by the reduplication of the cuticle over the caudal extremity in most individuals of both sexes.

(21) PHYSALOPTERA MAGNIPAPILLA Molin, 1860. (Text-fig. 31.)

Some of the excellently preserved type material in the collection of the Vienna Museum was examined.

The body appears smooth, but under high magnification the cuticle is seen to be provided with very delicate transverse striations. It is slightly reflected over the base of the lips, and in some females it was reflected over the whole of the tail in a manner similar to that seen in *Ph. præputialis*.

The cervical papillæ are small and spike-like, and pierce the cuticle about 150  $\mu$  behind the level of the hind end of the muscular œsophagus; from 75 to 100  $\mu$  further back on the ventral surface the opening of the excretory duct is found.

The lips are somewhat quadrangular, with large subdorsal and subventral external papillæ, and each is provided with two teeth of the same height; the outer tooth has a widened tip, whereas the median inner tooth is tripartite.

The œsophagus immediately follows the lips. It is straight, and forms in the female 1/5.5 and in the male 1/6.6 of the total body-length. Its anterior muscular part is nearly 1/10th of the whole organ, is slightly thinner, and is encircled in its posterior third by the nerve ring.

*Female.*

The females vary from 30 to 38 mm. long by .9 to 1.1 mm. broad; they are attenuated in their anterior fourth and posterior fifth, and the body is terminated by a bluntly conical tail 1/52nd of the body-length and having its caudal pores in its posterior half.

The vulva opens level with the surface, and its position divides the body in the ratio of 1:2.3; it leads into a straight muscular vagina nearly 2 mm. long by 80  $\mu$  thick. The egg-chamber is

slightly shorter, and about three times as broad as the vagina. The common trunk is about 1.1 mm. long and  $75\mu$  thick; its posterior end divides twice, in the same way as seen in *Ph. abbreviata*, to give rise to the four uteri.

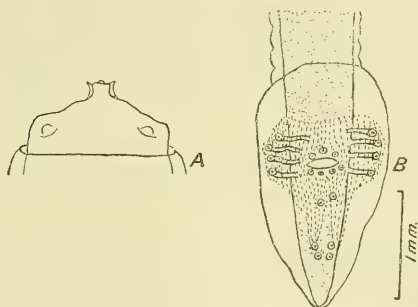
The eggs are small, oval, and thick-shelled, measuring on an average  $40\mu$  long by  $26\mu$  broad; when laid they are already fully embryonated.

### Male.

The males are much smaller than the females, and measure from 20 to 25 mm. long, with a maximum breadth of .7 to .85 mm. The body is attenuated in its anterior half, the posterior half being of uniform thickness.

The bursa is pointed and recurved ventralwards. The four pairs of pedunculated papillæ are equidistant, three pairs being pre-anal. The three pre-anal ventral papillæ are small, and are

Text-figure 31.



*Physaloptera magnipapilla* Mol.

A = Lateral view of lip.

B = Caudal extremity of male.

situated immediately in front of the anus. The first two pairs of post-anal ventral papillæ are also small and situated in a row in close proximity to the anus. The 3rd pair is larger and slightly obliquely placed; they divide the tail roughly into the ratio of 1:3. The 4th and 5th pairs are small and approximated to each other, and are situated just behind the middle of the tail. The ventral surface of the bursa is ornamented with longitudinal rows of tubercles.

The spicules are straight, tubular, pointed, and slightly unequal; the left is  $450\mu$  long by  $26\mu$  broad at its base, and the right is  $415\mu$  long by  $20\mu$  broad at its base.

Host: *Myrmecophaga bivittata*. Stomach. Brazil.

Types in bottle 4457 in the Vienna Museum.

My observations differ from those of von Drasche only in respect to the teeth; he states that the outer tooth is small, and in his figure shows it smaller than the inner tooth. In the worms

examined by me the two teeth were of the same size and fairly large.

The number of uteri and their mode of origin brings the species into the group characterised by *P. abbreviata*. It differs, however, from all the reptilian tetradelphoid forms by the shape of its outer tooth and by the presence of a large and tripartite inner tooth; this latter tooth is either absent—*Ph. colubri*—or represented only by a small spike-like tooth at the base of the outer tooth—*P. paradoxa*—in the reptilian forms.

The nature of the teeth and the presence of four uteri ally this species to *Ph. tumefaciens* Henry & Blanc, 1912, from which species it differs, however, by the different arrangement of its bursal papillæ, no reduplication of the cuticle over its tail, mode of origin of its uteri, and the presence of a common trunk portion in its unpaired female genitalia.

(22) PHYSALOPTERA QUADROVARIA Leiper, 1908. (Text-fig. 32.)

The types of this species, which were kindly placed at my disposal for study by Professor Leiper, consisted of six mature females and one male; the latter unfortunately had most of its bursal region broken off.

The parasites are stout, being thickest just behind their middle and attenuated towards both extremities. The cuticle shows a fine transverse striation, and is partly reflected over the lips.

The two cervical papillæ are situated laterally some distance behind the junction of the two œsophageal parts. In the male they are  $550\ \mu$  from the anterior end, and in the females slightly more than  $600\ \mu$ . The excretory duct opens ventrally at the same level or just behind the level of the cervical papillæ.

The lips are large and somewhat flattened in lateral view; each carries a large wedge-shaped external tooth with its tip slightly bent outwards, and two much smaller lateral teeth slightly split. Between the median and lateral teeth, on the inner face of the lip, there is a row of very small denticles. Internal to and attached to the base of the external tooth there is a small and spike-like internal tooth.

The œsophagus is relatively short, forming in the male  $1/7$ th and in the female about  $1/9$ th of the total body-length; it is straight, slightly thickening posteriorly, and its anterior end is differentiated into a short and narrow muscular part, about  $350\ \mu$  long in both sexes, and having the nerve ring in its posterior quarter.

*Female.*

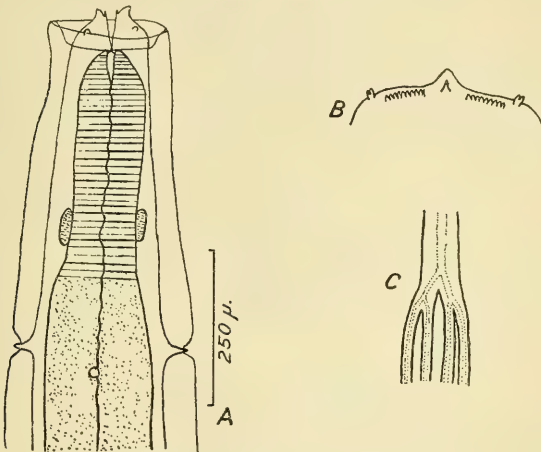
The specimens vary in length from 28 to 32 mm., with a breadth of .95 to 1.1 mm. The tail is relatively long and



pointed, forming  $1/45$ th of the total body-length, and has its caudal pores situated in its posterior third.

The vulva is situated on a slight elevation at the junction of the 1st and 2nd body fifths; it leads into a long and thick-shelled vagina 2.2 mm. long by  $95\ \mu$  broad. This vagina passes straight backwards to join the egg-chamber, which is also large and straight, measuring 1.8 mm. long by  $380\ \mu$  broad. The hind end of this chamber narrows sharply to join the common trunk, which is  $760\ \mu$  long and  $90\ \mu$  in diameter; its posterior end divides into two, each of which in their turn subdivide to give rise to the four uteri. These two primary branches are so short as to almost give the appearance that the uteri all arise at the same level.

Text-figure 32.



*Physaloptera quadrovaria* Leiper.

A = Anterior extremity of body.    B = Inner view of lip.  
C = Mode of origin of uteri.

The eggs are thick-shelled and oval, measuring  $51\ \mu$  long by  $36\ \mu$  broad; they embryonate *in utero*.

#### Male.

The solitary and incomplete male is 19.5 mm. long and  $750\ \mu$  thick. Part of the left spicule—the bursa is broken off just in front of the anus—is seen inside the body, but nothing remains of that of the right side. The remaining portion of the left spicule is long and filiform, measuring 1.3 mm. long. The spicules are probably very unequal.

Host: *Varanus niloticus*. Intestine. Sudan.

Discussion.—See *Ph. varani*.

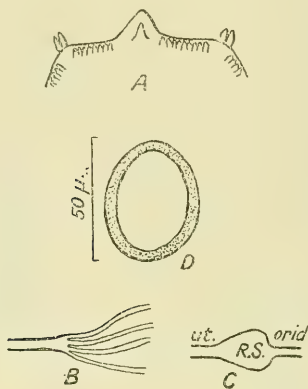
(23) *PHYSALOPTERA PARADOXA* von Linstow, 1908. (Text-figs. 33 & 34.)

Syn. *Ph. affinis* Gedoelst, 1916.

The primary study of this species is based on materials collected in the Zoological Society's Gardens from *Varanus albigularis*. All the specimens from the other hosts were kindly handed over to me by Professor Leiper for study and comparison. The material from *Varanus albigularis* consisted of about a dozen males and females, which had unfortunately been killed in formalin, so that the specimens were somewhat shrunken and coiled.

The shape of the body is very similar to that of *P. quadrovaria*, but is much smaller in size, mature females varying from 18 to

Text-figure 33.



*Physaloptera paradoxa* v. Linst.

A = Inner view of lip.                      B = origin of uteri.  
C = Receptaculum seminis.              D = Egg-shell.

24 mm. in length with a thickness of 750 to 870  $\mu$  in their posterior third, and the males from 14 to 18 mm. long by 450 to 500  $\mu$  broad in their posterior fifth.

The cuticle is coarsely annulated and, in addition, shows a very fine transverse striation; it is only very slightly reflected over the base of the lips. The cervical papillæ and excretory pore are situated in the same level behind the junction of the muscular and glandular cesophageal parts; in the male they are about 550  $\mu$  from the anterior end and in the female about 750  $\mu$ .

The lips are similar to those described for *Ph. quadrovaria*, except that lateral to each of the outer teeth there is another

row of small denticles on the inner surface parallel to the edge of the lip.

The muscular part of the œsophagus is thinner than the glandular part, and is encircled by the nerve ring at its base. The whole organ is short, and forms in the females  $1/7$ th and in the males nearly  $1/8$ th of the total body-length.

#### *Female.*

The vulva opens practically flush with the surface, there being only a slight trace of an elevation. Its position is post-œsophageal, and divides the body in the ratio of  $1:2.4$ ; it leads into a long and thick-walled vagina about 2 mm. long by  $100\ \mu$  broad; its most anterior portion is slightly twisted. The following egg-chamber is straight, and lies parallel to the intestine; it is slightly thicker than the vagina but shorter, measuring 1.2 mm. long by  $133\ \mu$  broad. The following common trunk is relatively short, and is thinner than the vagina; it is  $570\ \mu$  long and  $57\ \mu$  thick. From its posterior end the four uteri take their origin at the same level, but their cavities arise by a double subdivision of the unpaired duct. The uteri at first pass forwards to beyond the posterior end of the œsophagus, after which they bend backwards and fill the body almost to the posterior end.

The eggs are thick-walled, oval, and fully embryonated *in utero*; they measure  $50\ \mu$  long by  $35\ \mu$  broad.

The body is terminated by a relatively long and pointed tail, forming  $1/47$ th of the total length; its caudal pores are situated just behind its middle.

#### *Male.*

The caudal bursa is large and provided with well-developed alæ; its ventral surface is traversed by coarse cuticular elevations arranged in longitudinal rows. The anus is a large and transversely oval aperture, with a thickened rim, very prominent when viewed from the ventral surface; it is situated about  $850\ \mu$  from the tip of the tail.

The four pairs of pedunculated papillæ are equidistant from each other; two pairs are pre-anal and two pairs are post-anal in position; of the three pre-anal ventral papillæ the median one is situated slightly closer to the anus than the other two. Behind the anus there are five pairs of sessile papillæ: the 1st and 2nd pairs of these are small, and situated close together just behind the anus, one pair behind the other; the 3rd and 4th pairs are closely approximated, and found just in front of the middle of the tail; while the last pair is situated just posterior to the front margin of the posterior quarter of the tail.

The spicules are very unequal, and appear to vary in size; but these variations may be due to the difficulty found in measuring them. The right spicule is short, and varies from  $185$  to  $240\ \mu$

long, with a thickness of  $50\mu$  at its base; the left spicule is long and filiform, varying from 1.8 to 2.8 mm. long; it is about  $15\mu$  thick at its base; both spicules terminate in sharp tips.

Hosts: *Varanus albigularis*. Stomach. South Africa.

*Psammophis sibilans*. " Sudan.

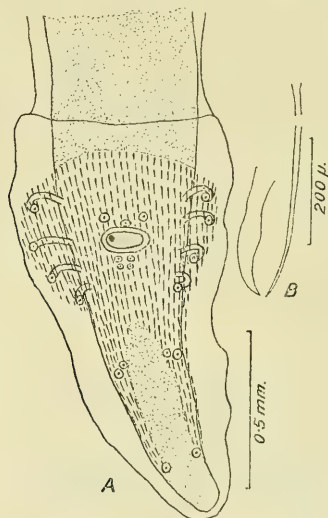
"Snake." " Nigeria.

"Colubrine snake." " Sudan.

"Snake." " Nigeria.

*Discussion*.—My observations differ slightly from those of Seurat (1914 b) made on parasites obtained from *Varanus griseus* and *Cerastes cornutus*. These differences apply to the spicules, which are  $100\mu$  and 1.92 mm. long for the right and left spicule respectively in Seurat's material, whereas in my material

Text-figure 34.



*Physaloptera paradoxa* v. Linst.

A = Caudal extremity of male.

B = Spicules (only part of left indicated).

the right spicule varied in length from 185 to  $240\mu$  and the left from 1.8 to 2.8 mm. Also the eggs in his specimens are  $10\mu$  broader than in mine. Despite these differences I believe the parasite to be the same, and the difference in size of the spicules can be accounted for in that it is not always possible to measure them correctly, as they generally take up a twisted course inside the body.

Von Linstow (1908), in his description of this species, draws attention to the absence of caudal alæ on the tail of the male, and for this reason gave it the name "*paradoxa*." Seurat (1914)

explains this absence by supposing that von Linstow was examining immature material, as he (Seurat) had in his possession immature specimens of *Ph. alata* in which the caudal alae were also absent. Unfortunately, I have not in my collection any Physaloptera in this condition, and consequently I accept Seurat's interpretation.

There is, however, another difference between von Linstow's observations and mine; this concerns the number of the post-anal ventral papillae. Von Linstow finds an extra pair present behind the second, whereas in my material there is no indication of these papillae, neither were they present in Seurat's (1914) material. It is therefore probable that von Linstow was mistaken in his observations, especially as my material and his are from the same host, both from South Africa, and there further appears no reason to doubt the identity of the two materials.

(24) PHYSALOPTERA VARANI Parona, 1889. (Text-fig. 35.)

The material on which the study of this species is based consists of three males collected from *Varanus bengalensis* and two females collected from *V. indicus*. I wish to express my indebtedness to Professor Leiper for placing this material at my disposal.

The body is attenuated towards both extremities, and shows a coarse transverse ringing in addition to a very fine transverse cuticular striation. The cuticle is partly reflected over the lips.

The cervical papillae are situated laterally a short distance behind the junction of the two oesophageal parts; on the same level or just posterior to it is the opening of the excretory gland.

The two lateral lips are large and tall. Each is provided with a large external tooth whose tip is slightly recurved; attached to it on its inner surface there is a small and membranous spike-like tooth, and on each side of it, towards the angles of the lips, there is a small bifid tooth. Externally each lip carries a large subdorsal and subventral papilla.

The oesophagus is long, and forms in the male  $1/6$ th and in the female  $1/5.5$  of the total body-length. Its anterior muscular part is slightly thinner than the following glandular part, and the nerve ring encircles it about  $80\ \mu$  from its base.

*Female.*

The two females are respectively 35 and 17 mm. long by 1 mm. and  $530\ \mu$  broad; the body is terminated by a pointed tail  $1/80$ th of the total length, with its caudal pores just behind its middle.

The vulva is non-protuberant, and is situated at the junction of the 1st and 2nd quarters of the body; it leads, in the smaller female, into a thick-walled vagina  $950\ \mu$  long by  $85\ \mu$  in diameter; this passes gradually into the egg-chamber, which is 1.8 mm. long and  $170\ \mu$  thick. The common trunk which follows it is 1.14 mm. long and  $50\ \mu$  in diameter. The first two parts pass



straight down the body, whereas the common trunk is recurved and passes forwards parallel to the other parts. The posterior end of the common trunk divides into two branches, each of which in their turn, after a distance of  $120\mu$ , subdivide to give rise to the connections of the four uteri.

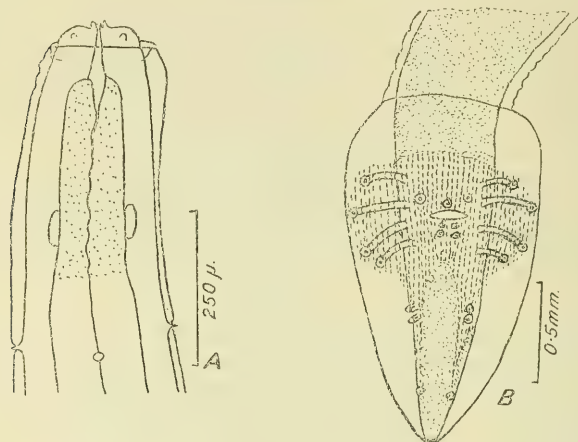
The eggs are oval and thick-shelled, and contain fully embryonated embryos before being laid. They are  $53\mu$  long by  $32\mu$  in diameter.

#### Male.

The males are respectively 12, 21, and 24 mm. long, the largest being  $800\mu$  thick in its posterior quarter.

The caudal bursa is large, and nearly twice as long as it is broad. The papillae are arranged in identically the same way as those described for *Ph. paradoxa*, as also are the tubercular

Text-figure 35.



*Physaloptera varani* Parona.

A = Ventral view of cephalic extremity.

B = Caudal extremity of male.

elevations. The outline of the bursa, however, is slightly different, its length and breadth being respectively relatively shorter and broader than in *Ph. paradoxa*.

The spicules are very unequal and bent, and both end in sharp points. The right is broad, with almost parallel edges except for its posterior tenth; it is  $342\mu$  long by  $25\mu$  broad at its base. The left spicule is long and filiform, 2.1 mm. long by  $14\mu$  broad at its base.

Hosts: *Varanus bengalensis*. Stomach. Ceylon.

*Varanus indicus*. " India.

Discussion.—Seurat (1917 a) considers this species to be identical with *Ph. paradoxa* v. Linst. and *Ph. quadrovaria* Leiper.

After a study and comparison of these three species, I hold that, although they are nearly related, they must be regarded as distinct species. *Ph. varani* differs from *Ph. paradoxa* by its longer œsophagus, longer trunk, mode of origin of the four uteri, and the absence of a denticular ridge on the inner side of each lip. It differs from *Ph. quadrovarya* by its longer œsophagus, shorter tail of the female, less evolved type of origin of the uteri, and also by the absence of denticles on the inner surface of the lips.

*Ph. varani* appears to be very closely related to *Ph. abbreviata*, as redescribed by Seurat (1914 *b* and 1917 *a*), with which species it agrees in the female genitalia. It appears, however, to differ from *Ph. abbreviata* in its larger size, absence of denticles on the inner surface of the lips, relatively shorter bursa, and larger spicules. I have unfortunately not been able to examine and compare any examples of *Ph. abbreviata*.

*Ph. pallaryi* Seurat, 1917, seems to be a near relative of *Ph. varani*, from which species it can, however, be very easily distinguished by its much shorter left spicule, the conformation of the circumcloacal area, and by the position of the vulva in front of the posterior limit of the œsophagus.

Parona's (1889) description differs from my findings in that he mentions and figures the presence of four pairs of post-anal ventral papillæ, the last three pairs of which are equidistant from each other, the 1st pair being situated immediately behind the anus. I think an error has crept in his observations: namely, that he has missed one pair of small papillæ just behind the 1st, and has misjudged the distance separating the 2nd and 3rd pairs in his figure. I am led to this view because I think his specimens could not have been well preserved, as he shows the caudal alæ having a lobulated border, a state of affairs which I have noticed to take place in contracted specimens. I do not think there can be any doubt as to the identity of the materials, although Parona's description is so incomplete that it can apply to quite a number of Physaloptera.

(25) PHYSALOPTERA ANTARCTICA v. Linstow, 1899. (Text-figs. 36 & 37.)

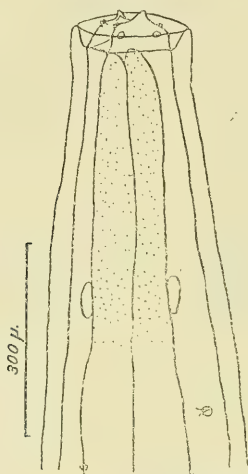
Syn. *Ph. alba* Stoss., 1902.

#### *Female.*

Mature and fully-grown females are about 45 mm. long and 950  $\mu$  broad. The body is of more or less uniform thickness, only tapering slightly towards the anterior end. The body is terminated by a short tail about 440  $\mu$  long. The cuticle is roughly ringed, and between these rings a very fine cuticular striation is observed under high-power magnification; the cuticle anteriorly is partly drawn over the lips. The cervical papillæ are lodged in shallow pits in the cuticle, and are situated about 650  $\mu$

from the anterior end; the excretory pore is seen on the ventral surface about  $95\ \mu$  further back; it leads into the excretory duct, which passes into a gland lying against the ventral surface of the œsophagus. The two lateral lips are each surmounted by a large triangular tooth, slightly recurved at its tip; applied to the inner surface of each is a small spike-like tooth. On either side of the median tooth, in the lateral angles of each lip, there is seen another tooth, much smaller than the terminal tooth and split almost to its base; just below these and on the outer surface of the lip there is a conspicuous papilla. The lips are immediately followed by the œsophagus, which is straight and thickens slightly towards its posterior end. It is about  $4.7\text{ mm.}$  long or  $1/9.5$  of the body-length, and is divided into a short and narrower

Text-figure 36.

*Physaloptera antarctica* v. Linst.

Latero-ventral view of cephalic extremity.

anterior part about  $475\ \mu$  long and a longer posterior glandular part. The first part is surrounded near its base by the large nerve ring.

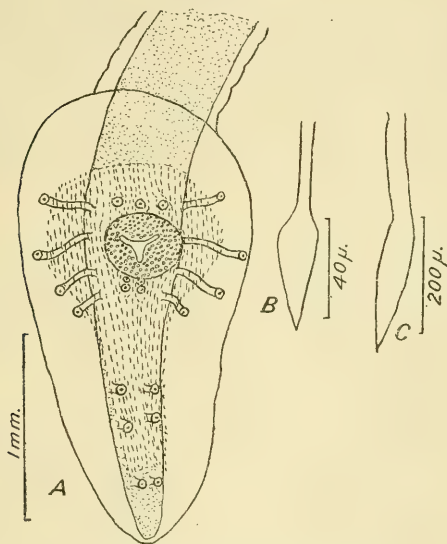
The chief characteristics of the female genitalia is the presence of four uteri. The vulva is a circular aperture, flush with the surface and situated at about the junction of the 1st and 2nd quarters of the body. It leads into a short and slightly coiled vagina, very muscular and about  $90\ \mu$  in diameter. It is followed by the egg-chamber, about  $259\ \mu$  in diameter; the hind end of this chamber constricts suddenly, so that the common trunk has about the same diameter as the vagina. The common trunk divides posteriorly into two branches, and these after a short distance subdivide again. The four uteri thus formed may first

pass forwards to beyond the junction of the œsophagus and intestine and then pass backwards, or they may pass backwards directly. The uteri are more or less parallel, and their hinder ends pass gradually into the receptacula seminis, about  $380\mu$  long by  $150\mu$  broad. The receptacula seminis pass abruptly into the oviducts,  $38\mu$  in diameter, which soon join the ovaries; the latter pass forwards, taking more or less a convoluted course.

*Male.*

The males are slenderer than the females, fully-grown forms being about 32 mm. long and  $750\mu$  broad. The body is only

Text-figure 37.



*Physaloptera antarctica* v. Linst.

A = Caudal extremity of male.    B = Tip of left spicule.  
C = Right spicule.

slightly attenuated anteriorly. The cuticle is of the same character as the female, and the cervical papillæ occupy relatively the same position, being situated a short distance beyond the junction of the muscular and glandular portions of the œsophagus. The excretory pore is situated ventrally about  $130\mu$  further back than the cervical papillæ. The lips are as described for the female.

The first part of the œsophagus is thinner than that following, measures about  $500\mu$  long, and is surrounded at its base by the nerve ring. The total length of the œsophagus is 3.55 mm. or 1/9th of the body-length.

The bursa is large, being about  $2\frac{1}{4}$  mm. long by  $1\frac{1}{4}$  mm. broad across the cloaca. The lateral expansions are well developed, and the central portion of the ventral surface is covered by longitudinal rows of spike-like tubercles. The anus is a triradiate aperture, situated in the centre of a more or less circular cushion like a swelling, about  $420\ \mu$  in diameter, and itself covered with small tubercles. On either side of it there are four elongate papillæ, implanted equidistant from each other. Anterior to the cushion there are three ventral papillæ of equal size and situated in a row; immediately posterior to the cushion there are two small pairs of ventral papillæ. There are three other pairs of ventral papillæ further down the tail, of which the middle pair is nearer to the anterior than to the posterior pair. These last three pairs of papillæ are each provided with a short stalk.

The spicules are unequal, that of the left side being longer than that of the right side. The left spicule measures  $1504\ \mu$  long by  $19\ \mu$  broad at its base; at its tip it widens out to form a kind of spear-head  $64\ \mu$  long by  $18\ \mu$  broad. The right spicule is stout, and measures  $410\ \mu$  long by  $33\ \mu$  broad at its base. In its posterior two-fifths it becomes slightly widened out, after which it gradually tapers to a point.

Hosts: *Varanus varius*. } Stomach. Australia.  
*Python spilotes*. }

My material has been identified as *Ph. antarctica* v. Linst. because of the general agreement of the measurements of my material with those of von Linstow's; the only important difference is the relative length of the tail of the female; von Linstow gives it as  $1/54$ th of the body-length, whereas in my material it forms only about half this length.

Only two species have so far been described from Australian lizards—namely, the species described by von Linstow and *Ph. alba* described by Stossich (1902). Irwin-Smith (1922) considers these species to be the same, and I am inclined to agree with her. Unfortunately, I have not been able to examine material from any of the hosts from which these two species were obtained, but from the brief descriptions and figures given by von Linstow and Stossich it appears probable that they are identical.

*Ph. antarctica*, because of the nature of its labial teeth and mode of origin of the four uteri, is closely related to *Ph. abbreviata*, *Ph. varani*, and *Ph. pallaryi*; it is, however, very easily distinguished from all these by the configuration of its male bursa and by the difference in size and shape of the spicules. I have given an extract of both von Linstow's and Stossich's descriptions in Part II.

(26) PHYSALOPTERA COLUBRI (Rud., 1819), Diesing, 1851. (Text-fig. 38.)

The types of this species, deposited in the Vienna Museum, consisted of two immature females and the fragments of another worm; the specimens were slightly shrunken.



The cuticle is finely striated transversely, and is partly reflected over the lips; the cervical papillæ are situated about  $100\ \mu$  behind the level of the hind end of the muscular œsophagus, and the excretory pore about  $75\ \mu$  further back.

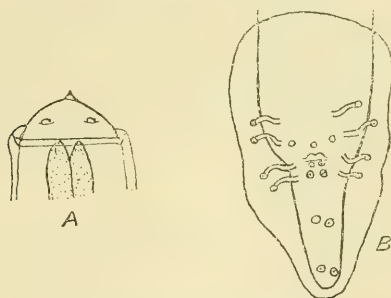
The lips are rounded, and each is surmounted by a single large terminal tooth, no other teeth being present. Externally each lip carries a small subdorsal and subventral papilla.

The œsophagus forms nearly  $1/4\cdot6$  of the body-length; its anterior muscular part is thinner than the rest, and it is encircled by the nerve ring in its posterior third; it forms just less than  $1/10$ th of the whole organ.

#### *Female.*

The two specimens measure respectively 7 and 8 mm. long by  $350$  and  $360\ \mu$  broad; the body is attenuated in its anterior half, and it is terminated behind by a relatively long and bluntly rounded tail, which is turned up dorsally in both specimens; it

Text-figure 38.



*Physaloptera colubri* (Rud.), Dies.

A = Lateral view of lip.

B = Caudal extremity of male. (After v. Drasche.)

is about  $1/30$ th of the body-length, and its caudal pores are situated in its posterior third. The vulva is only very slightly protuberant, and its position divides the body into the ratio of  $1 : 2\cdot5$ ; it leads into a vagina bent on itself and measuring  $1\frac{1}{4}$  mm. long by  $55\ \mu$  thick; the egg-chamber is  $320\ \mu$  long by  $145\ \mu$  in diameter, and is also bent on itself; the following common trunk is of about the same length as the egg-chamber, and is about  $50\ \mu$  broad; its posterior end divides into two, each of which, after a distance of  $240\ \mu$ , again divides into two to give rise to the four uteri.

No eggs were observed, the specimens being immature.

#### *Male.*

The following description of the male bursa is based on von Drasche's description and drawing, no males being available for personal study.

The caudal expansions are well developed, and the four pairs of stalked papillæ are situated in two groups, two pairs being pre-anal and two pairs post-anal. The three pre-anal ventral papillæ are of the same size, the middle one being nearer the anus than the other two.

There are four pairs of post-anal ventral papillæ, of which the 1st is small and situated immediately behind the anus; the 2nd, 3rd, and 4th pairs are equidistant, the 2nd being situated at the level of the last pair of stalked papillæ, and the last near the tip of the tail.

Host: *Coronella austriaca*. Intestine. Australia.

Types in bottle 4451 in the Vienna Museum.

It is probable that when the male of this species is re-examined, it will be found that there are five pairs of post-anal ventral papillæ, and that the extra papilla will be situated near the 1st pair just behind the anus.

(27) *PHYSALOPTERA SIMPLICIDENS*, sp. n. (Text-fig. 39.)

The material examined consisted of three females, two of which were immature, one small male, and one larger male which had its bursa broken off.

The cuticle is finely striated, and is slightly reflexed over the lips; the cervical papillæ are situated in small concavities just behind the junction of the muscular and glandular parts of the œsophagus. The excretory pore is situated on the ventral surface about  $60\mu$  further back.

The lips are somewhat flatly conical in side view, and each bears a large triangular tooth, slightly recurved outwards; no other teeth were observed. Each lip carries two papillæ, one subdorsal and one subventral, on its outer surface.

The œsophagus is short, and in the female forms  $1/13$ th and in the male  $1/8$ th of the body-length; its anterior muscular part forms about  $1/9$ th of its length, and is distinctly separated from the following glandular part; it is encircled by the nerve ring in its posterior quarter.

*Female*

The females are about 44 mm. long and  $950\mu$  broad, and are attenuated towards both extremities; this is only slightly evident posteriorly where the body is terminated by a short and conical tail, forming  $1/105$ th of the body-length. The vulva divides the body into the ratio 1:3.3; it leads into a muscular vagina  $1.3$  mm. long by  $95\mu$  in diameter; this in turn passes gradually into the egg-chamber, which is  $1.7$  mm. long by  $325\mu$  broad; the following common trunk is short, and divides into two branches, each of which after a distance of  $200\mu$  divides again to give rise to the four uteri.

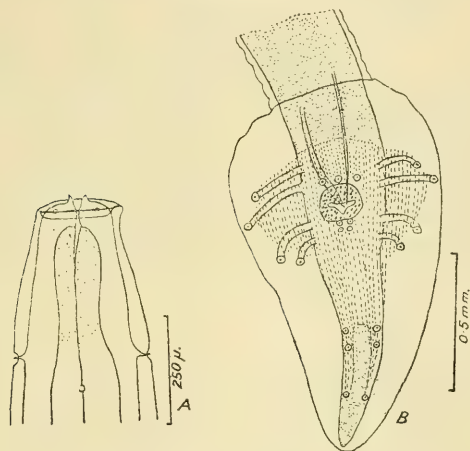
The eggs are oval and very thick-shelled, measuring on an average  $55\mu$  long by  $41\mu$  broad, with a shell  $9\mu$  thick; they are fully embryonated *in utero*.

*Male.*

The males are respectively 14 mm. and 21 mm. long; they are attenuated only towards the anterior end; the maximum breadth of the larger male is just in front of the bursa, where it is  $725\mu$  broad.

The bursa is large, and is nearly twice as long as it is broad; it forms about  $1/10\cdot7$  of the body-length. The arrangement of the papillae is similar to that found in *Ph. antarctica* v. Linst., except that the lateral stalked papillae are arranged in two groups, the 1st and 2nd pairs forming a pre-anal group, and the 3rd and 4th pairs forming a post-anal group.

Text-figure 39.

*Physaloptera simplicidens*, sp. n.

A = Ventral view of anterior extremity of body.

B = Caudal extremity of male.

The spicules are slightly unequal, the left being slightly longer and slenderer than the right; their lengths and breadths are respectively  $510\mu$  by  $38\mu$  and  $410\mu$  by  $50\mu$ ; both end in fine points, the right, however, being slightly swollen just behind its middle.

Host: "Sleeping Lizard." Australia.

Types in the Helminthological Department of the London School of Tropical Medicine.

*Affinities.*—The presence of four uteri and a single tooth allies this species to *Ph. colubri* (Rud.), from which species it is, however, distinguished by its much larger size, its relatively much shorter œsophagus, and by the difference in number and arrangement of the post-anal ventral papillae.

GROUP **Polydelphys.**

(28) **PHYSALOPTERA TURGIDA** Rudolphi, 1819. (Text-fig. 40.)

Syn. *Turgida turgida* (Rud., 1819), Travassos, 1920.

*Spiroptera turgida* (Rud., 1819), Duj., 1845.

The material studied consisted of some excellently preserved specimens in the collection of the Vienna Museum, and of three tubes of material in the collection of Prof. Leiper.

The cuticle is slightly inflated, and is partly reflected over the lips; it is transversely striated by very fine striæ; the cervical papillæ pierce the cuticle just behind the level of the muscular œsophagus, and from 200 to 300  $\mu$  further back is the opening of the excretory gland.

The two lateral lips are semi-conical in lateral view; each is surmounted by a large triangular outer tooth having its tip slightly bent outwards; immediately internal to it is a large membranous tooth of equal height and tripartite; no lateral teeth are present. Each lip carries two external papillæ, one subdorsal and one subventral.

The œsophagus is long and straight, widening gradually posteriorly; in the females it varies from  $1/4.8$  to  $1/5.5$  of the total length, and in the male from  $1/3.9$  to  $1/5.9$ ; its muscular portion is thinner than the rest, and forms in the female  $1/10$ th and in the male  $1/8$ th of the whole organ. The nerve ring encircles it in its posterior third.

*Female.*

Adult and fully mature females are large and stout, measuring as much as 55 mm. long by 3 mm. broad in their posterior half. The body is attenuated in its anterior half, but posteriorly the thickness is more or less uniform until the vicinity of the anus, where the body tapers suddenly to form a pointed tail  $1/45$ th to  $1/56$ th of the total body-length, and whose caudal pores are situated in its posterior third.

The position of the vulva varies considerably, but in all cases it was situated behind the end of the œsophagus; it divides the body in the ratio of 1:2 to 1:4.4. The vagina is thick-walled, short, and passes straight back; it is just less than 1 mm. long by 95  $\mu$  thick. It passes directly into a larger egg-chamber of about the same length and about 230  $\mu$  broad; from the posterior end of this chamber a number of uteri take their origin; because of the complicated manner in which they were entwined, it was not always possible to determine the exact number, but in two specimens it was definitely seen that the one had 11 and the other had 14 uteri. The uteri pass down the body, coiled round each other, almost to the posterior end, when they recurve and join up with the receptacula seminis, which in their turn are united to the ovaries by means of short and thin oviducts. The oviducts pass forwards again to about the middle of the body.

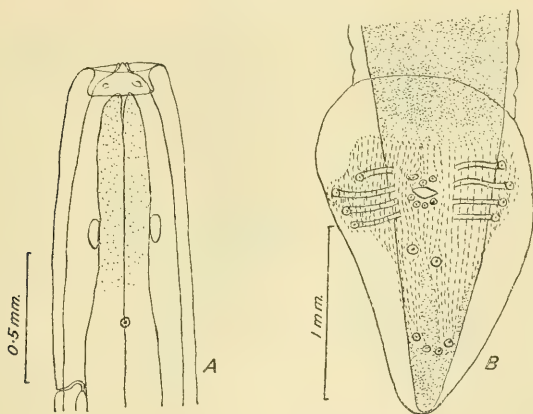
The eggs are oval and thick-shelled and relatively narrow, measuring  $48\ \mu$  by  $29.5\ \mu$ .

*Male.*

The males are smaller than the females, apparently mature specimens measuring from 21 to 32 mm. long by .950 to 1.25 mm. thick; the body is much more attenuated anteriorly than in the females, this thinning beginning from about the posterior third.

The bursa is large, and has well-developed lateral expansions; the four pairs of pedunculated papillæ are equidistant from each other, two pairs being pre- and two pairs being post-anal in position. Of the three pre-anal ventral papillæ, the middle one is situated nearer the anus than the other two. Behind the anus there are five pairs of ventral papillæ; of these the 1st and

Text-figure 40.



*Physaloptera turgida* Rud.

A = Lateral view of cephalic extremity.

B = Caudal extremity of male.

2nd pairs are situated immediately behind the anus in a row, the 3rd pair is slightly oblique in position, and the 4th and 5th are situated close together. The ratio of the distances separating pairs 2 and 3, 3 and 4 to 5, and 5 to the tip of the tail is as 1:2:1.

The spicules are of equal length, short, straight, and tubular; each is about  $410\ \mu$  long by  $32\ \mu$  broad at its base.

The ventral surface of the bursa is covered with longitudinal protuberances.

Hosts: *Didelphys cancrivora*. Stomach. Brazil.  
 "Manicon." " West Indies.

*Didelphys virginiana*. " Michigan.

*Affinities*.—See *Ph. dilatata*.



(29) *PHYSALOPTERA DILATATA* Rudolphi, 1819. (Text-fig. 41.)

Syn. *Spiroptera dilatata* (Rud., 1819), Duj., 1845.

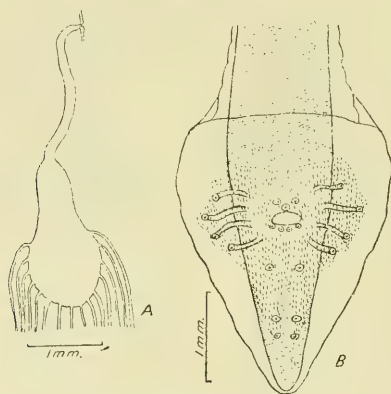
Two males and two females were examined from bottle 4454 in the Vienna Museum. The females were somewhat shrunken, but otherwise the material was in an excellent condition.

The cuticle is finely striated transversely, and is loosely attached to the body; it is reflected over the base of the lips.

The cervical papillæ are situated about  $290\ \mu$  behind the level of the posterior limit of the muscular œsophagus, and the excretory pore about another  $200\ \mu$  further back.

The two lips are large and semi-rectangular, with projecting dorsal and ventral corners. Each is surmounted by a large conical external tooth, and a tripartite inner tooth of the same

Text-figure 41.



*Physaloptera dilatata* Rud.

A = Terminal portions of female genitalia.

B = Caudal extremity of male.

height but semi-membranous. No additional teeth are present. Externally each lip has a subdorsal and a subventral dome-like papilla.

The œsophagus is remarkable for its difference in relative length in the two sexes; in the two male specimens examined it formed respectively  $1/4.3$  and  $1/4.8$  of the total body-length; in the females it is relatively only half this length, forming in the one  $1/8.6$  and in the other  $1/7.5$  of the total length. Its muscular part is thinner than the following glandular, and forms about  $1/10$ th of the whole organ; it is encircled by the nerve ring at the junction of its third and last quarters.

#### *Female.*

The females are large and stout, the two specimens measuring

respectively 55 and 90 mm. long, with a maximum breadth of 1.9 and 2.9 mm. respectively; the body is attenuated only in its anterior half, the posterior half being of the same thickness, except for the tail region, where the body tapers abruptly to form a conical tail  $1/85$ th of the total length.

The vulva opens very far forwards, being situated in front of the middle of the œsophagus; its position in one specimen divided the body in the ratio of 1:22. It leads into a comparatively straight vagina  $2\frac{1}{4}$  mm. long by  $115\ \mu$  broad. The following egg-chamber is club-shaped, 2 mm. long by about  $840\ \mu$  broad at its widest part; many uteri take their origin from the outer edge of the club; 15 were present in the one specimen, and in the other at least 12 could be made out.

The eggs are oval and thick-shelled, averaging  $39\ \mu$  long and  $27\ \mu$  broad.

### Male.

The males are smaller than the females, measuring respectively 47 and 55 mm. long by 1.45 and 1.6 mm. broad. The body has its maximum breadth just in front of the bursa, and from here the body attenuates gradually towards the anterior end.

The bursa is broad and sharply recurved ventralwards; it forms about  $1/16$ th of the body-length, and its ventral surface is covered with longitudinal rows of tubercles. The four pairs of pedunculated papillæ are equidistant, three pairs being pre-anal and the 2nd and 3rd pairs are much longer than the other pairs; of the pre-anal ventral papillæ, the middle one is slightly larger and is situated nearer the anus. There are five pairs of post-anal ventral papillæ, of which the 1st and 2nd pairs are small and situated in a row immediately behind the anus; the 2nd, 3rd, and 4th pairs are equidistant from each other, while the distance between the 4th and last pair is only about a third the distance separating the two preceding pairs.

The spicules appear to be short and equal, but unfortunately the tip of the right spicule was broken off in both specimens, so that it was not possible to determine its correct length; the left spicule was straight and pointed, and measured  $655\ \mu$  long by  $57\ \mu$  broad at its base; the base of the right spicule had the same thickness as that of the left side.

Host: *Lagothrix humboldtii*. Stomach. Brazil.

*Affinities*.—This species appears to be closely related to *Ph. turgida*, with which species it agrees in the form of the lips and teeth, general size, and in the anatomy of the female genitalia. It is, however, readily distinguished from this species by the position of the vulva, the difference in the relative length of the œsophagus in the two sexes, and by the position of the 4th and 5th post-anal ventral papillæ on the male bursa.

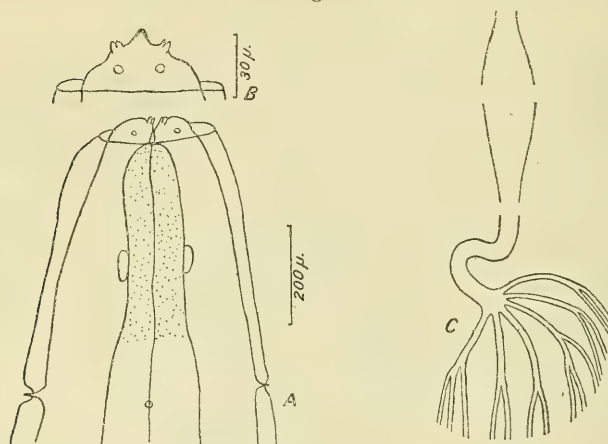
(30) *PHYSALOPTERA CAPENSIS*, sp. n. (Text-figs. 42 & 43.)

The material on which this study is based consisted of one female, two males, and portions of two males.

The cuticle is very finely striated transversely, and is only very slightly reflected over the base of the lips.

The lips are large, and each has on its outer lateral border two dome-like papillæ. The median external tooth is large and is situated on the summit of the lip; its tip is bluntly rounded; immediately internal to it there is another tooth of the same height, but having its tip slightly notched; towards the angles of each lip there is an additional tooth, fairly large, which is generally bifid and may sometimes be irregularly trifid. On

Text-figure 42.

*Physaloptera capensis*, sp. n.

A = Ventral view of anterior extremity of body.

B = Outer lateral view of lip.

C = Terminal portions of female genitalia.

either side of the median tooth there is another bifid tooth, very small and somewhat difficult to make out; it is situated about midway between the median and lateral teeth.

The cervical papillæ and excretory pore are situated at the same level, about  $120\ \mu$  behind the junction of the two œsophageal parts.

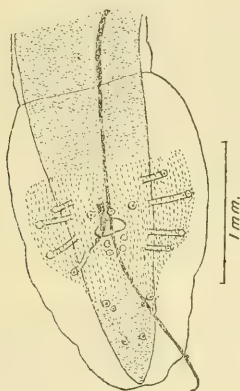
The muscular part of the œsophagus forms about  $1/11$ th of the total length of the œsophagus; it is slightly narrower than the following part, and is surrounded in its middle by the nerve ring. The whole œsophagus forms just less than  $1/5$ th of the total body-length in the male and  $1/10$ th in the female.

*Female.*

The solitary female is robust, having somewhat the appearance of a short ascarid. It is 56 mm. long, and 1.7 broad in its middle; it is attenuated only very slightly anteriorly.

The vulva is situated flush with the surface and 15.85 mm. from the anterior end; it leads into a long vagina 3.62 mm. long and  $152\mu$  broad; this vagina, except for a loop at its end, passes straight down the body to join the egg-chamber; this is also very long but not very broad, measuring 4.86 mm. long by  $343\mu$  in diameter. The end of the chamber joins the common trunk, which is 2.19 mm. long and about as thick as the vagina. The rest of the genitalia are remarkable for the number and mode of origin of the uteri; there are 14 uteri arising from six branches, which unite to form the common trunk; four of these branches

Text-figure 43.

*Physaloptera capensis*, sp. n.

Caudal extremity of male.

give rise each to two uteri, whereas each of the remaining two branches give rise to three uteri.

The tail is pointed and  $950\mu$  long; the caudal pores open  $380\mu$  from its tip.

The eggs are oval and thick-shelled, measuring  $55\mu$  long by  $32\mu$  broad, and shell  $4\mu$  thick.

*Male.*

The males are much slenderer than the females, measuring 24 mm. long by  $900\mu$  broad just behind their middle; they are slightly attenuated anteriorly.

The caudal bursa is large, and twice as long as it is broad; it forms about 1/11th of the body-length; the caudal alæ are well developed, and are supported by the four pairs of pedunculated papillæ, of which two pairs are pre-anal and two pairs post-anal

in position. On the ventral surface there are three pre-anal papillæ immediately in front of the anus, and five pairs of post-anal papillæ. The 1st and 2nd of these last are found close together near the anus; the 3rd and 4th are closely approximated to each other, and are inserted in the middle of the tail; the last pair is situated midway between them and the caudal extremity; the whole ventral surface of the bursa is covered by longitudinal rows of tubercles.

The spicules are unequal, that of the left side being over six times as long as that of the right. The right spicule is fairly stout, measuring  $57\mu$  at its base and gradually tapering to a point; it is  $420\mu$  long. The left spicule is also pointed, but much slenderer; it is  $2.7\text{ mm.}$  long by  $27\mu$  broad at its base.

Host: *Xerus setosus*. Stomach. South Africa.

The types to be deposited in the British Museum of Natural History, London.

The mode of origin of the uteri, in conjunction with their number, give this species a unique position in the genus.

The general character of the vagina, egg-chamber, common trunk, and eggs are typical for the genus, so that the presence of numerous uteri is not a sign of very close affinity to the polydelphoid species *Ph. turgida* and *Ph. dilatata*.

(31) *PHYSALOPTERA* sp. (Text-fig. 44.)

The study of this species is based on a single male  $15\text{ mm.}$  long and  $.65\text{ mm.}$  broad. It was collected from the stomach of a Bandicoot which had died in the Gardens of the Zoological Society of London.

From the middle forwards the body becomes attenuated, but behind the middle the body is of a uniform thickness. The cuticle is finely striated transversely, and is reflexed over the lips so as to completely enclose them. The cervical papillæ are found  $457\mu$  from the head end, *i. e.* at the junction of the two œsophageal parts. The excretory pore is situated just behind them.

The mouth is bounded by two large and somewhat conical lips, each surmounted at its apex by a large and triangular outer tooth and immediately internal to it by a median tripartite tooth, of the same height as the outer tooth, but less chitinated. Two external papillæ are present on each lip.

The œsophagus is  $3.77\text{ mm.}$  long; its muscular part is thinner and  $400\mu$  long, and the nerve ring encircles it just behind its middle.

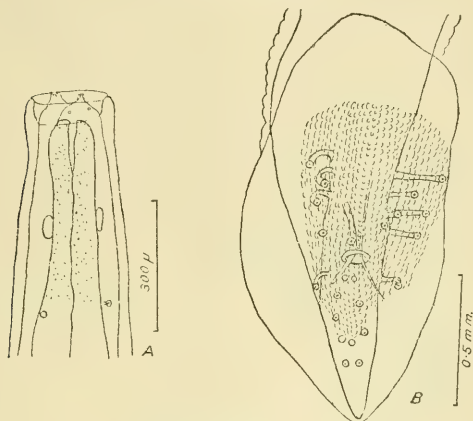
The caudal bursa is twice as long as it is broad, and it forms  $1/9\text{th}$  of the body-length. Its chief characteristic is the irregular arrangement of its papillæ. Of these there are four stalked papillæ on the right side and six on the left. Those of the right side are arranged in a pre-anal group of three, far removed from the anus, and a post-anal papilla; those of the left side are arranged in a pre-anal group of five and a single post-anal papilla. The three pre-anal ventral papillæ are far removed from each



other, the centre one being large and situated nearest to the anus. There are five pairs of post-anal ventral papillæ, situated more or less equidistant from each other; the 2nd, 3rd, and 4th pairs of these are obliquely situated across the tail, whereas the 1st and last pairs are arranged transversely.

The spicules are unequal, the left being longer and slenderer than the right. The right spicule is  $370$  by  $50\mu$  thick at its base; it tapers to a rounded tip. The left spicule is  $523\mu$  long by  $20\mu$  broad at its base, and tapers to a fine point.

Text-figure 44.



*Physaloptera* sp.

A = Latero-ventral view of cephalic extremity.

B = Caudal extremity of male.

The ventral surface of the bursa is ornamented with longitudinal rows of somewhat rounded tubercles.

Host: *Perameles nasuta*. Stomach. Australia.

I have not attempted to classify this species, because only a single specimen was available for study, and the arrangement of its bursal papillæ differed so much from the typical that I consider the specimen to be abnormal.

## PART II.

### GROUP *Didelphys*.

#### (32) *PHYSALOPTERA RARA* Hall & Wigdor, 1918.

Male unknown; length of female 24 mm., maximum thickness 1.34 mm.

Anterior extremity somewhat attenuated. Cuticle strongly annulated, and first annulation behind the head forms a sort of collar, into which the head is partly sunk.

Two lateral lips large, each carrying three prominent inner median teeth and a somewhat smaller external tooth. Each lip with three external papillæ.

Length of œsophagus 1.16 mm.; its muscular part  $526\ \mu$  long. Nerve ring near base of muscular œsophagus.

Vulva 3.63 mm. from anterior end. Vagina  $880\ \mu$  long. Egg-chamber and common trunk together 2.16 mm. long. Two uteri. Tail blunt and  $420\ \mu$  long.

Host: *Canis familiaris*. Duodenum. Michigan.

Hall and Wigdor suggest that this may be an accidental parasite of the Dog. From the remarkable shortness of the œsophagus and the relative length of its muscular part, I suggest that this worm is abnormal, which could easily be accounted for if it was parasitic in a wrong host.

### (33) *PHYSALOPTERA TACAPENSIS* Seurat, 1917.

Length of male 15.6 mm., female 22.3 mm.

Cervical papillæ subsymmetrical, at same level as excretory pore immediately behind the muscular œsophagus. External tooth strongly chitinised and truncated; internal tooth of same height. Œsophagus  $1/4$  in the male and  $1/4.6$  in female of body-length. Female tail short and conical; male tail conical.

Vulva immediately in front of end of œsophagus. Vagina 2.3 mm. long, egg-chamber 1.02 mm. long; common trunk absent. Two uteri. Receptaculum seminis very long. Eggs with very thick shell ( $7\ \mu$ );  $56\ \mu \times 30\ \mu$ .

Male caudal bursa with longitudinal cuticular ornamentations. Character and arrangement of bursal papillæ exactly as those in the species described by Seurat (1917 b) as *Ph. clausa*.

Right spicule  $240\ \mu$  long, thick, and thimble-shaped; left spicule  $360\ \mu$  long, slenderer, with conical tip.

Host: *Ctenodactylus gundi*. Stomach. Sud-Tunisien.

From Seurat's description this species appears to be so closely related to his *Ph. clausa* that it appears hardly warrantable to separate the two. The similarity of the teeth, shape of spicules, and arrangement of male caudal papillæ appear to me to be of far greater weight than the slight differences of the relative positions of the vulva, relative lengths of the œsophagus, lengths of the spicules, positions of the cervical papillæ and excretory pore, and the larger egg, all of which differences may very well be due to the fact that the one parasite is about twice the size of the other. In a given species of *Physaloptera* taken from the same host, the differences in size between one adult and another is often very marked, and consequently there is always a certain amount of difference between the individual specimens.

### (34) *PHYSALOPTERA GETULA* Seurat, 1917.

Length of male 16.3 mm., female 18.5 mm.  $\times 970\ \mu$  thick.

Body stout, attenuated anteriorly; cervical papillæ sub-

symmetrical, far posterior to end of muscular œsophagus and just in front of excretory pore. External tooth conical, slightly shorter than the internal tooth.

Vulva may be found behind œsophagus, but generally it opens in front of its posterior termination, even so far forwards as its middle. Two uteri arise directly from base of egg-chamber. Receptaculum seminis short and ovoid, not constricted off from the uterus.

Egg? Tail short, digitiform, with rounded tip.

Body of male smaller and slenderer than that of female. Bursa ornamented with spines. Three large papillæ just in front of anus; 3rd pair of post-anal papillæ at the level of the 5th pair of external papillæ.

Spicules unequal, right larger and shorter with bent tip, left slenderer and straight. 350 and 480  $\mu$  long respectively.

Host: *Mus rattus*. Stomach. Morocco.

(35) PHYSALOPTERA BREVIVAGINATA Seurat, 1917.

Only immature female known; 9.8 mm. long  $\times$  444  $\mu$  thick.

External tooth strongly chitinised with broad base (surbaissée) and bent outwards. Internal tooth tripartite, and higher than the external tooth; its middle part is bicuspid. Two papillæ to each lip. Œsophagus 1/4th, tail 1/35th of body-length; tail has a rounded tip, and the caudal pores are in its posterior third.

Vulva immediately in front of middle of body, 2.3 mm. from anterior extremity. Vagina very short, 300  $\mu$  long; egg-chamber 600  $\mu$  long, and its posterior end passes directly into the two uteri.

Host: *Vespertilio kuhlii*. Stomach. Bou-Saâda.

(36) PHYSALOPTERA ALATA, var. CHEVREUXI Seurat, 1914

Has same character as *Ph. alata*; differs by its smaller size and very posterior position of the cervical papillæ and excretory pore.

*Male* 7 mm. long  $\times$  515  $\mu$  thick. Muscular œsophagus 260  $\mu$ . Œsophagus 1/4th of body-length. Cervical papillæ 370 and 360  $\mu$  from anterior end; excretory pore 384  $\mu$ .

*Female* (immature). Length 8 mm.; tail long (310  $\mu$ ) and conical. Vulva a short distance behind end of œsophagus.

Host: Hawk. Bône.

(37) PHYSALOPTERA ALATA, var. NOUVÉLI Seurat, 1915.

Large nematodes with robust body and regularly attenuated anteriorly. Cervical papillæ subsymmetrical, situated more or less at the level of the hind end of the muscular œsophagus. Two lateral lips, each with a large triangular external and pointed tooth, and a very small internal tooth with three tips. Œsophagus short, 1/6th of body-length.

*Male*. Length 22–28.5 mm.  $\times$  900  $\mu$  thick. Tail conical and slender, 1.165 mm. long. Circumcloacal area covered with small

cuticular tubercles. (Arrangement of the papillæ as in *Ph. alata*.) Three pre-anal sessile papillæ arranged in a triangle. Four pairs of post-anal ventral papillæ; the 1st and 2nd pairs of these are slightly stalked, and are found on the posterior lip of the cloaca; the last pair is situated just behind the middle of the tail. Five pairs of lateral stalked papillæ grouped about the cloaca, the last inserted at the level of the 3rd pair of post-anal ventral papillæ. Right spicule robust and large,  $550\ \mu$  long; left spicule slenderer, feebly chitinated, and longer.

*Female* 33 mm. long  $\times$  1.055 mm. thick. Tail long, conical, and pointed. Caudal pores in its anterior third. Œsophagus 5.61 mm. long. Vulva in front of termination of Œsophagus, 3.8 mm. from anterior end. Unpaired female genitalia very long; vagina 2.15 mm. long and directed backwards; egg-chamber 3.125 mm. long; trunk  $500\ \mu$  long, and divides posteriorly to give rise to two uteri. Receptacula seminis pyriform,  $600 \times 325\ \mu$ . Egg elliptical, thick-shelled, and embryonated; they measure  $50 \times 25\ \mu$ .

Hosts: *Aquila chrysaetos*. } Œsophagus. Bou-Saâda.  
*Accipiter nisus*. }

(38) *PHYSALOPTERA SUBALATA* Schneider, 1866.

Length of male 32 mm.

Tips of lips very prominent. Outer tooth longer than inner tooth; edges of smaller teeth quite parallel, and pointed at the tip. Four pairs of stalked circumcloacal papillæ. Three sessile pre-anal papillæ, the middle one nearer the anus; three pairs behind the anus, of which the last two pairs are close together, one pair behind the other, and the last pair nearer the mid-line; the other pair is situated at about the junction of the 1st and 2nd tail thirds.

Host: *Falco* sp. Stomach. Brazil.

With regard to the nature of the teeth, Schneider's description differs from his figure; he states that the outer tooth is larger than the inner, and in his figure shows the outer tooth very much smaller. I take his figure to represent the correct nature of the teeth.

Seurat (1914 c) tentatively referred to this species some *Physaloptera* which he obtained from the stomach of a Buzzard, San Martino, Corsica. Briefly he describes this material as follows:—Large and robust body. Two lips, each with a small and cuneiform outer tooth and a large tripartite inner tooth. Œsophagus  $1/4.5$  in male,  $1/6$ th in female of body-length. Vulva in anterior third of body, 3 mm. behind Œsophagus. Vagina 1 mm., egg-chamber  $750\ \mu$  long; trunk divides to give origin to two uteri.

Bursa with four stalked circumcloacal papillæ. Three pre-anal ventral papillæ form a triangle; two pairs immediately behind anus, 3rd pair in middle of tail.

Spicules unequal; left  $840\ \mu$  long, slender, and pointed; right less than  $400\ \mu$  long, and thicker.



## (39) PHYSALOPTERA CROSI Seurat, 1914.

Male 22 mm. long by 660  $\mu$  thick, female 12–22 mm. long.

Two lips, large, each with two external papillæ. External tooth large and triangular; inner median tooth very small and tripartite. Cervical papillæ situated immediately behind level of nerve ring.

Œsophagus  $1/6$ th in male,  $1/4$ th in female of body-length.

Male bursa plus well-developed alæ, and ornamented with tubercles. Arrangement of its papillæ as in *Ph. galinieri* and *Ph. subalata*, except that an unpaired sessile papilla is present between the last pair of ventral papillæ. Spicules equal, 300  $\mu$  long.

Tail of female short, with caudal glands opening in front of its middle. Vulva in anterior third, 1 mm. behind œsophagus. Vagina shorter than egg-chamber, which is 1200  $\mu$  long  $\times$  300  $\mu$  broad; trunk 400  $\mu$  long, and divides to give rise to the connections of the two uteri. Eggs  $55 \times 25$   $\mu$ , embryonated.

Host: *Accipiter nisus*. Stomach. Mascara.

## (40) PHYSALOPTERA GALINIERI Seurat, 1914.

Length, male 21 mm., breadth 780  $\mu$ ; length, female 17–34 mm. by 1.05 mm. thick.

Two lateral lips, each with a large and very conspicuous tripartite inner tooth.

Œsophagus  $1/6$ th in male and  $1/7$ th in female of body-length. Cloaca 925  $\mu$  from end of tail in male. Five pairs of stalked papillæ, of which the anterior 4 pairs are arranged circumcloacally, and the last some distance further back. Eleven ventral papillæ, with short stalks and approaching mid-ventral line; of these, 3 are pre-anal, 4 immediately behind the anus in a transverse row, 2 at the level of the posterior pair of circumcloacal stalked papillæ, and 2 midway between the posterior stalked papillæ and tip of tail.

Spicules short, 360 and 380  $\mu$  long.

Vulva a short distance in front of middle of body, far removed from hind end of œsophagus. Ovijector passes forwards; vagina 2 mm. long; egg-chamber oval, 600  $\mu$  long; trunk 200  $\mu$  long. Two uteri, one of which passes forwards and then recurves backwards, whereas the other passes straight back. Receptaculum seminis sharply constricted off from oviduct and uterus, rounded; diameter 240  $\mu$ . Eggs  $65 \times 35$   $\mu$ .

Host: Aigle. Œsophagus and stomach. Aïn-Oussera.

## (41) PHYSALOPTERA LEPTOSOMA (Gervais, 1848), Seurat, 1917.

Syn. *Strongylus leptosomus* Gervais, 1848.

*Ph. chameleontis* Geddoelst, 1916.

Length of male 7.8–20 mm., of female 12.5–45 mm.

Two lips; external tooth cuneiform, slightly knobbed at its tip; internal tooth spike-like; lateral teeth bicuspid (these teeth more



or less as in *Ph. paradoxa*, except that inner median tooth is larger); inner denticulate border reduced and interrupted in places.

Muscular oesophagus very short. Oesophagus  $1/6$ th in male,  $1/10$ th in female. Cervical papillae asymmetrical, just behind muscular oesophagus.

Vulva at level of end of oesophagus or just posterior: vagina 2.2 mm. long, egg-chamber  $925\ \mu$  long, trunk  $500\ \mu$  long. Two uteri. Receptaculum seminis  $400\ \mu$  long. Eggs  $52 \times 35\ \mu$ .

Tail of female elongate and digitiform, with its caudal pores in its posterior third.

Circumcloacal area of male with small tubercles arranged longitudinally; in adult males these are spined.

Male bursa lanceolate; 4 pairs circumcloacal stalked papillae. Thirteen ventral papillae; of these, 3 in front of anus, the lateral 2 being shortly stalked; 2 pairs immediately behind anus; 2 pairs just in front of middle of tail, the anterior pair being stalked; 2 papillae at posterior third of tail. Spicules very unequal; right short and thick,  $156 \times 35\ \mu$ ; left slender and twelve times as long as the right, 1.92 mm.

Hosts: *Uromastix acanthinurus* and *U. a.* var. *nigriventris*.

Stomach and oesophagus. Algeria.

*Varanus griseus*. Stomach and intestine. Algeria.

#### (42) PHYSALOPTERA CHAMAELEONTIS Gedoelst, 1916.

Syn. *Ph. leptosoma* (Gervais), Seurat, 1917.

Length of male 13.4 mm., of female 22 mm.  $\times 815\ \mu$  thick.

Two hemispherical lips, each with a triangular external tooth. No internal teeth.

Oesophagus of male 1.9 mm., of female 3.7 mm. long; bursa 1.44 mm. long; spicules unequal, right  $370\ \mu$ , left 2.1 mm. long. Arrangement of bursal papillae as in *Ph. affinis*. Vulva divides body into ratio of 1:4. Two uteri. Eggs  $56-63 \times 40-44\ \mu$ .

Host: *Chamaeleon gracilis*. Stomach. Belgian Congo.

I agree with Irwin-Smith (1922) that this species is the same as *Ph. leptosoma* (Gervais), Seurat, 1917. The close similarity between Gedoelst's and Seurat's descriptions is very striking. The slight differences in the lengths of the spicules, length of oesophagus, and position of the vulva can very well be accounted for as individual variations.

### GROUP Tetradelphys.

#### (43) PHYSALOPTERA NUMIDICA Seurat, 1917.

Male unknown. Length of female 31.9 mm., thickness  $950\ \mu$ .

Two lips, each with a very large external tooth, a very small inner median tooth, and two bicuspid lateral teeth. Cervical papillae subsymmetrical and situated far behind the muscular oesophagus, at the level of the excretory pore. Tail short and

conical; caudal pores in its posterior third. Muscular œsophagus short; œsophagus  $1/8$ th of body.

Vulva in anterior quarter of body, 3.8 mm. behind œsophagus. Vagina 2.16 mm. long, straight; egg-chamber long; trunk long, and divides dichotomously to give rise to four uteri. Receptaculum seminis oval.

Host: *Dipodillus campestris*. Stomach. Bou-Saâda.

(44) PHYSALOPTERA ABBREVIATA Rudolphi, 1819.

Syn. *Spiroptera abbreviata* (Rudolphi), Duj., 1845.

Body robust. Two lateral lips large. External tooth large, wedge-shaped, and truncated at its tip. Three inner teeth as in *Ph. paradoxa*. Muscular œsophagus thick; nerve ring at its posterior end. Œsophagus long,  $1/3.6-1/5.4$  in female,  $1/4-1/5.5$  in male of body-length.

*Female*. Length 7.8–20 mm., attenuated towards both extremities. Tail conical, with caudal pores just behind its middle. Position of vulva variable, opening either in front of or behind end of œsophagus; divides body into ratio of 1:2–1:6. Unpaired female genitalia, very long (3.5 mm.), consist of vagina, egg-chamber, and relatively long trunk. Four uteri arise by dichotomous division of trunk. Receptaculum seminis  $150 \times 120 \mu$ , sharply constricted off from both uterus and oviduct. Eggs  $50-60 \times 37 \mu$ .

*Male* 7.5–11 mm. long. Tail elongate. Caudal alæ large. Cuticular projections small and arranged in rows. Cloacal lips non-salient. Arrangement of papillæ as in *Ph. paradoxa*. Spicules very unequal; left long and filiform, 2 mm. long; right short and stout,  $180 \times 45 \mu$ . Both pointed.

This description is based on Seurat's (1914 *b*, 1917 *a*) descriptions of the species from worms obtained from the stomach of *Lacerta ocellata*. Bou-Saâda.

(45) PHYSALOPTERA PALLARYI Seurat, 1917.

Length of male 8.1–10.8 mm., length of female 12.4 (larvæ) to 25 mm.

Two lips, each with its anterior border slightly trilobed. Two external papillæ very small. External tooth triangular, pointed, and recurved. Internal denticulate border formed of twenty sharp denticles. Cervical papillæ at junction of two œsophageal parts; excretory pore at same level or just posterior. Tail of female very short and rounded; caudal pores in its posterior fifth.

Œsophagus long,  $1/5$ th in the male,  $1/6$ th in the female of body-length.

Vulva  $260-1200 \mu$  in front of end of œsophagus. Vagina short,  $350 \mu$  long; egg-chamber 1.2 mm. long; trunk  $650 \mu$  long, and divides dichotomously to give rise to four uteri. Eggs  $65 \times 32 \mu$ .

Male tail massive, with rounded extremity. Anus opens on a large cushion,  $100\mu$  in diameter and covered with large warts. First two pairs of stalked papillæ at the same level; 3rd pair at the level of the cloaca; 1st pair post-anal ventral papillæ just behind cloaca, last pair  $85\mu$  from caudal extremity. Spicules unequal: right pointed and thick,  $150\mu$  long; left slender,  $260\mu$  long.

Host: *Agama bibroni*. Stomach and intestine. Morocco.

(46) *PHYSALOPTERA AFFINIS* Gedoelst, 1916.

Length of male 11–13.2 mm., of female 18.7–20.7 mm.  $\times$  .8 mm.

Two lateral lips. External tooth large and triangular; no median internal tooth. Œsophagus of ♂  $1\frac{1}{4}$  6, of ♀  $1\frac{1}{5}$  6– $1\frac{1}{6}$  6 of body-length. Bursa 1.4 mm. long; 2 pre-anal and 2 post-anal stalked papillæ; 3 pre-anal ventral papillæ arranged in a triangle; 2 pairs papillæ close behind anus; 2 pairs close together in middle of tail; 1 pair at junction of last tail quarters.

Spicules unequal, 2.2 mm. and  $270\mu$  long; club-shaped plus a conical tip.

Vulva just behind œsophagus or as much as 2 mm. further back. Four uteri. Eggs  $56 \times 40\mu$ .

Host: *Psammophis sibilans*. Intestine. Belgian Congo.

From Gedoelst's description this species appears to be the same as *Ph. paradoxa* v. Linst. I have examined *Physaloptera* from the same host, and these have been found to belong to von Linstow's species, and consequently Gedoelst's species must be relegated to a synonym of *Ph. paradoxa*.

## GROUP Polydelphys.

(47) *PHYSALOPTERA TORRESI* (Travassos, 1920).

Syn. *Turgida torresi* Trav., 1920.

Length of male 35 to 40 mm., of female 70 to 90 mm.; thickness of male 1 to 1.5 mm., of female 2 to 2.5 mm.

Two subtriangular lips, each with four external papillæ and one apical and median papilla. Three teeth present on the tip of each lip, the median being larger and more internal in position than the other two; it is  $17\mu$  in length. Lips  $85\mu$  high. Œsophagus claviform, 6 to 8 mm. in length, and its muscular part is 400 to  $430\mu$  long.

Vulva situated about midway down œsophagus. Egg-chamber gives rise directly to 9 to 11 uteri. Receptaculum seminis pyriform,  $870\mu$  long and  $380\mu$  thick. Eggs 42 to  $49\mu$  long by  $28\mu$  in diameter. Anus 780 to  $870\mu$  from the posterior extremity.

Male caudal bursa with well-developed ake. Four pairs of lateral circumcloacal pedunculated papillæ. Three sessile papillæ in front of the anus and two pairs of sessile papillæ in a row immediately behind the anus; three further pairs equidistant from each other in the anterior half of the tail. Spicules

subequal and weakly chitinated, 430 to 520  $\mu$  long. Anus about 2 to 4 mm. from the caudal extremity.

Host: *Agouti paca*. Stomach. Bahia, Brazil.

*Discussion*.—This species appears to be very closely related to *Ph. dilatata* Rud., 1819, the only notable difference being the position of 3rd, 4th, and 5th pairs of ventral post-anal papillæ in the male. In *Ph. torresi* these are equidistant from each other, and are situated in the anterior half of the tail, the distance between the 2nd and 3rd pairs being small; in *Ph. dilatata* the distances between the 2nd and 3rd, 3rd and 4th pairs are about equal and long, while that between the 4th and 5th pairs is only about half this distance.

Travassos describes and figures five external papillæ to each lip, but I very much doubt whether his observation is correct, as in all the species of this genus examined by me I have never seen more than two; he also mentions the presence of five similar papillæ in his description of *Ph. turgida*, but, having re-examined my specimens of this species, I still maintain that only two external papillæ are present.

There seem to be some inaccuracies or misprints in Travassos' description of this species. He writes "ovejector com vagina claviforme longa de cerca de 46 mm. de comprimento." I think this should be 4.6 mm., as it is hardly likely that this organ would be about half the length of the worm. Further, with regard to the ventral pre-anal papillæ of the male, the description reads "3 pares situados imediatamente acima do anus." As he figures the usual three papillæ in front of the anus, I think this sentence is intended to convey the fact that three papillæ, not three pairs, are situated in this position. Because of this error, the number of paired papillæ is given as 12 instead of 10 pairs in addition to an unpaired papilla.

With reference to the position of the anus in the male, the description reads that it is "a cerca de 2, a 4 mm. da extremidade posterior." In his French translation this sentence is rendered "a environ 2.4 mm. de l'extrémité postérieure." I am accepting the original to be what Travassos meant, although from the construction of the two sentences it would appear that the translation probably describes the true state of affairs.

It is not perhaps out of place here to draw the attention of those consulting Travassos' original description of this species to the fact that the French translation does not always give a correct rendering of the Portuguese text.

#### Forms with undetermined number of uteri.

(48) *PHYSALOPTERA CAUCASICA* v. Linstow, 1902.

Male 14.22 mm. long  $\times$  .71 mm. broad; female 27 mm. long by 1.14 mm. thick.

Cuticle unringed. Lips with four submedian papillæ, and large cone-shaped external teeth. Œsophagus 1/5th of body-length.



Male bursa broad anteriorly and narrowed behind; small tubercles on its ventral face. The spicules are unequal, right short and broad, left long and filiform; measure .62 mm. and 1.76 mm. long respectively. One pre-anal pair of papillæ (the median probably missed) and five post-anal pairs of ventral papillæ; the arrangement of these papillæ is similar to those found in *Ph. mordens*, except that the relation of the 3rd and 4th pairs to the ventral mid-line is the reverse to that found in *Ph. mordens*. Four pairs of lateral stalked papillæ.

Female tail rounded, 1/53rd of body-length. Vulva in the region of union of the 1st and 2nd body sixths. Egg  $57 \times 39 \mu$ .

Host: *Homo sapiens*. Intestine. Caucasus.

(49) *PHYSALOPTERA DIGITATA* Schneider, 1866.

Length of male 20 mm., of female 27 mm.

Outer tooth small, inner tooth larger than outer, with its tips rounded. Vulva 4 mm. from head end. Of the inner bursal papillæ, 3, 4, and 5 are more or less in a line on the ventral surface. Distance between 4 and 5 smaller than between 3 and 4. Distance from 5 to tip of tail more or less equal to the distance between 3 and 5; 1 and 2 immediately behind anus. Three pre-anal papillæ in a triangle. Four pairs of stalked papillæ; the distance between the most anterior two pairs greater than that separating the others.

Host: *Felis concolor*. Stomach. Brazil.

*Ph. terdentata* Mol., 1860, was described from the same host, but it appears to be different from *Ph. digitata* Schn., as shown by the difference in arrangement of its post-anal sessile papillæ. The nature of their teeth is, however, very similar.

(50) *PHYSALOPTERA BREVISPICULUM* v. Linstow, 1906.

Male 11.1 mm. long  $\times$  .95 mm. thick; female 11.4 mm. long  $\times$  1.06 mm. thick. Each lip with three small peaks (teeth?) on its summit. A preputium-like thickening over the tail is present.

Œsophagus 1/6.5, tail in male 1/9.4, in female 1/22.3 of body-length. Spicules very short, feebly curved, .79–.81 mm. long. Eggs  $36 \times 31 \mu$ .

Host: *Felis rubiginosa*. Stomach. Ceylon.

(51) *PHYSALOPTERA GEMINA* v. Linstow, 1899.

Length, male 11.4, female 19 mm.  $\times$  .53 mm. thick.

Two large conical external teeth; small lateral teeth; more smaller ones internally.

Œsophagus 1/5.9, tail of male 1/19th, of female 1/35th of body-length.

Bursa pointed; 4 pairs lateral stalked papillæ arranged in two groups, 2 pairs pre-anal and 2 pairs post-anal. Eleven ventral papillæ, of which 3 are in a pre-anal row, 2 in a row just behind



the anus, 4 stalked and in a transverse row just in front of middle of tail, 2 stalked and at the junction of last tail quarters.

Eggs  $52 \times 32 \mu$ .

Host: *Felis catus domesticus*. Stomach and intestine. Egypt.

(52) PHYSALOPTERA CESTICILLATA Somsino, 1889.

Length  $1\frac{1}{2}$ –3 mm. and more, slightly attenuated anteriorly, obtuse behind. Two retractile lips, with teeth on its inner front, and with at least one well-developed lateral papilla. A well-defined collar over the lips.

*Male*. Bursa of variable size, elongate and bent inwards. Four pairs of lateral pedunculate papillæ, and six pairs of ventral sessile papillæ plus two unpaired papillæ, one of which is pre-anal, and the other between the last pair of ventral post-anal papillæ. Except for the posterior unpaired papillæ, the arrangement of the papillæ is similar to that found in *Ph. papillotruncata*. Ventral surface of bursa with longitudinal rows of spikes.

*Female* immature. Tail mucronate and anus  $500 \mu$  from its tip.

Host: *Canis cerdo*. Stomach. Egypt.

(53) PHYSALOPTERA TORQUATA Leidy, 1856.

Males unknown. Females .25–.5 inches long by .02 inches thick (3–6 lines  $\times$  .25 of a line).

Body cylindrical, attenuated anteriorly; a conspicuous and narrow collar round the head; lips half conical, each with a pair of lateral papillæ and a group of four teeth on its apex, of which one is external to the others. Tail short, conical, obtuse, recurved from the anal aperture.

Host: *Meles labradorica*. Stomach. [America.]

Stossich (1889) lists this species under Sp. Inq., but the nature of the lips and the collar round the head, together with the nature of the teeth, strongly suggest that this species is a true *Physaloptera*.

(54) PHYSALOPTERA MEPHITES Solanet, 1909.

Host: *Mephites suffocans*. Buenos Aires.

(The description of this species, published in the 'Revista del Centro d. Estados d. Agronomia y Veterinaria,' Buenos Aires, was not available for reference.)

(55) PHYSALOPTERA ELEGANTISSIMA Stossich, 1902.

Length of female 50–60 mm. Male unknown.

Body large, cylindrical, and attenuated anteriorly. A large more or less imbutiform cuticular expansion embracing most of the cephalic region except the lips. Two lateral lips, large, and each has three large papillæ—one central and two lateral. External tooth large and conical, supplemented by two subequal denticles. Tail conical and rounded. Eggs smooth and elliptical with very thick shell.

Host: *Ratelus capensis*. Stomach. Eritrea.

(56) *PHYSALOPTERA GUIARTI* Garin, 1913.

Length 35 mm., breadth 2 mm.

Body cylindrical, elongate, and yellowish in colour; transversely striated. Anterior extremity with chitinous expansions. Teeth absent.

Male caudal extremity bent, with margin of alæ lobulated and corrugated; anal aperture in middle of bursa. Four pairs of circumcloacal papillæ. No internal papillæ.

Host: *Leptonychotes weddelli*. Stomach. S. Pole.

From Garin's brief description and crude drawing, this parasite is a *Physaloptera*, but the absence of teeth and internal papillæ on the tail of the male is very remarkable, and suggests the possibility of their having been overlooked.

(57) *PHYSALOPTERA CŒLEBS* v. Linstow, 1897.

Male 7 mm. long  $\times$  .51 mm. thick. Female unknown.

Œsophagus  $1/4.6$ , tail  $1/15.4$  of body-length.

Four pairs of lateral stalked papillæ. Three pre-anal papillæ arranged in a triangle. Five pairs of post-anal ventral papillæ, of which the last two pairs are stalked; pairs 1 and 2 just behind last pair of lateral papillæ; pairs 3, 4, and 5 in posterior third of tail.

Host: *Centetes ecaudatus*. Madagascar.

(58) *PHYSALOPTERA DISPAR* v. Linstow, 1904.

Length of male 16.6 mm. by .53 mm. broad; length of female 25 mm. by .95 mm. thick.

Two rounded lips surrounded by a cuticular collar. External tooth rectangular, with two small papillæ on either side; further back there is a larger papilla on either side. Œsophagus in male  $1/4.9$ , in female  $1/6.2$  of body-length.

Tail in both sexes rounded, and forms  $1/19$ th in the male and  $1/26$ th in the female of the body-length.

Caudal bursa of male with four pairs of elongately stalked papillæ; five sessile papillæ round the anus, one being pre-anal and four being post-anal; four further pairs of post-anal papillæ, of which the most anterior pair is just behind the level of the last pair of stalked papillæ, the 2nd and 3rd pairs close together at about the middle of the tail, and the last towards the tail tip. Spicules very unequal; right broad and .35 mm. long, the left slenderer and .62 mm. long.

Vulva divides the body into ratio of 3:8; eggs thick-shelled and embryonated,  $57 \times 39 \mu$ .

Host: *Erinaceus albiventris*. Stomach. Nigeria.

Seurat (1917 *b*) has identified this species with his specimens of "*Ph. clausa*." If von Linstow's description of the lips and arrangement of the bursal genital papillæ is correct, then this species cannot be regarded as the same as Seurat's specimens. Consequently, I think that until von Linstow's specimens have

been re-examined, his and Seurat's specimens must be treated as separate species.

(59) *PHYSALOPTERA INCURVA* v. Linstow, 1908.

Length of male 20 mm. by .75 mm. broad; female 47 mm. long by 1.58 mm. thick.

Two lips, dorsal and ventral; each with three teeth.

Œsophagus of male  $1/7.6$ , of female  $1/8$ th, tail of male  $1/22$ nd, of female  $1/235$ th of body-length.

Male bursa with four stalked papillæ—an unpaired pre-anal ventral papilla and three pairs of equidistant post-anal papillæ.

Spicules unequal, right .36 mm. long and broad, left .57 mm. long and narrow.

Vulva divides body into ratio of 34 : 59. Eggs  $57 \times 39 \mu$ .

Host: *Erinaceus frontalis*. Stomach and intestine. Kalahari.

It is doubtful whether von Linstow's observations in connection with the lips are correct. As all the other characters are typically those of the genus, it is probable that the lips are lateral in position and not dorsal and ventral.

(60) *PHYSALOPTERA CIRCULARIS* v. Linstow, 1897.

Length of male 15.2 mm.; length of female 24 mm. by 1.9 mm. thick.

Two lips, each with two rounded swellings internally, and three external papillæ.

Œsophagus of male  $1/4.3$ , tail of male  $1/15.4$ , tail of female  $1/61$ st of body-length.

Four pairs of circumcloacal stalked papillæ; one pair of sessile papillæ in front of, and an unpaired papilla just behind anus; three pairs of post-anal ventral papillæ, of which pairs 1 and 2 are close together at about the junction of the first two quarters of the tail, and the 3rd at about the middle of the tail.

Eggs with very thick shells,  $49 \times 33 \mu$ .

Host: *Mus rattus*. Stomach Madagascar.

It is quite possible that von Linstow missed an unpaired pre-anal sessile papilla and four small sessile papillæ just behind the anus. If this should later be found to be the case, then there would be reasonable ground for supposing this species to be either the same as, or very closely related to *Ph. muris-brasiliensis* Dies.

(61) *PHYSALOPTERA RUWENZORII* Parona, 1907.

Length of male  $9-9\frac{1}{2}$  mm., of female 14-17 mm.

Body attenuated for a short space anteriorly. Large lips with small papillæ. Teeth large and conical. Œsophagus  $1/6$ th of body-length.

Male caudal bursa large, with large circular expansion anteriorly and conical terminal portion; cuticular ornamentations absent;

four pairs of lateral and circumcloacal stalked papillæ; a large pre-anal unpaired ventral papilla; behind anus two pairs of ventral papillæ and a large unpaired papilla in front of them. Spicules unequal, pointed and slightly bent.

Tail of female long and attenuated. Vulva divides body into ratio of 1:2; it is slightly raised and papillate. Eggs oval, thick-shelled, containing partially developed embryos.

Hosts: *Arvicanthus abyssinicus*. Intestine. Fort Portal, Africa.

*Epimys ugandæ* (*Mus ugandæ*). Intestine. Fort Portal, Africa.

(Compiled partly from Parona and Hall's (1916) descriptions.)

## (62) PHYSALOPTERA SCIURI Parona, 1898.

Length of male 16 mm., of female 17-32 mm.; breadth of male .5 mm., of female .5-1 mm.

Two large and semicircular lips, with foliaceous external tooth.

Caudal bursa of male large and lanceolate; 4 pairs of lateral stalked papillæ situated circumcloacally; a large unpaired papilla close behind the anus; 2 pairs of ventral papillæ situated marginally and at about the middle of the tail; a pair of small ventral papillæ near the tip of the tail. The bursa is ornamented with numerous tubercles. The anus is large and circular, and has a scalloped and raised edge.

Tail of female obtuse. Vulva non-protuberant, and divides the body more or less into the ratio of 1:2. Single uterine tube. Eggs small and spherical, with a diameter of 16-22  $\mu$ .

Host: *Sciurus melanogaster*. Stomach and intestine. Mentawai.

As Hall (1916) has pointed out, Parona's observations with regard to the uteri is probably incorrect; in all other Physaloptera in which the number of uteri has been determined they are never less than two.

## (63) PHYSALOPTERA INERMIS v. Linstow, 1906.

Length of male 21.5 mm. by 1.26 mm. thick; length of female 51 mm. by 1.62 mm. thick.

Oesophagus of male 1/3.8, of female 1/8.5, tail of male 1/21st, of female 1/425th of body-length.

Bursa with four stalked papillæ on either side and four pairs of equidistant ventral and post anal papillæ; the most anterior of these are situated at about the middle of the tail. Longitudinal striations on alæ.

Spicules 2.37 mm. long.

Vulva divides body into ratio of 11:17. Eggs  $47 \times 26 \mu$ .

Host: *Sciurus prevosti*. Stomach. Koenigsberg.



(64) *PHYSALOPTERA CITILLI* (Rud., 1819), Hall, 1916.

Syn. *Spiroptera citilli* Rud., 1819.

Male unknown; female 7-13 mm. long by 400  $\mu$  thick.

"Body curved. Anterior extremity very slightly attenuated. Head rounded, continuous with the body, and with the cuticle inflated. Mouth with two large lips. Six head papillæ, of which there are two conical papillæ situated on each side near the angle of contact of the two lips, and one spherical papilla at the base of each lip. Cuticle densely striated transversely. Posterior extremity of female obtuse. Vulva in anterior portion of body."

Host: *Citellus citellus*. Stomach.

Hall (1916) transferred this species to *Physaloptera*, partly on the opinion expressed by Molin and partly because the description could apply to a member of this genus. I follow both these authorities, and consequently list it as a valid member of the genus *Physaloptera*.

(65) *PHYSALOPTERA PYRAMIDALIS* v. Linstow, 1879.

Length of male 18 mm. by 1 mm. thick; length of female 50 mm.  $\times$  1.5 mm. thick.

Two pyramid-like lips, dorsal and ventral in position. Outer tooth pointed, inner tooth of same size and tripartite. Œsophagus 1/5.7, tail 1/28th in male and 1/55th in female of body-length. Two pre-anal and two post-anal stalked papillæ in caudal extremity of male; in addition 4 pairs of unstalked papillæ, of which one pair is pre-anal and 3 pairs post-anal.

Vulva at junction of 1st and 2nd body fifths. Eggs very thick-shelled, 42  $\times$  33  $\mu$ .

Host: *Cholæpus didactylus*. "An den Sehnen der Zehen." Surinam.

This species appears to differ from *Ph. papillotruncata* by its pointed outer tooth and by the more anterior position of the vulva; nevertheless I am inclined to think that this species is identical with or a variety of *Ph. papillotruncata*.

It is possible that von Linstow is mistaken in the position of the lips, and that they are really lateral.

(66) *PHYSALOPTERA LIMBATA* Leidy, 1856.

Length .5 inch, breadth .02 inch (6 lines  $\times$  .25 of a line).

Mouth two-lipped and surrounded by an elevated linear margin. Caudal extremity of male alated and having four pairs of divergent and stalked papillæ.

Host: *Scalops canadensis*. Stomach. Philadelphia.

Molin (1860) lists this species under *Sp. Inq.*; however, in view of the fact that there are two lips surrounded by what may be interpreted as a cuticular collar, and that the male bursa is alated and has four (pairs) of stalked papillæ, I think there is good ground for supposing that this species is a true *Physaloptera*.



(67) *PHYSALOPTERA NASILIONIS* Geddoelst, 1916.

Larvæ: length 6 mm. Two lateral lips. External tooth triangular. Œsophagus 2.23–2.33 mm. long. Nerve ring in posterior quarter of muscular Œsophagus. Tail conical and blunt,  $215\ \mu$  long.

Host: *Nasilio brachyrhynchus*. "Tissu conjonctif." Belgian Congo.

(68) *PHYSALOPTERA BILABIATA* (Creplin, 1829), Dujardin, 1845.

Two large lips, prominent and obtuse. Body much attenuated anteriorly. Caudal extremity of male reflexed, alate, elliptical, with four stalked papillæ. Tail of female conical and obtuse.

Length, ♂ 0.025, ♀ ultra 0.025; breadth 0.001.

Host: *Lanius minor*. Intestine. (Extracted from Stossich's Monograph.)

(69) *PHYSALOPTERA MEGALOSTOMA* Creplin, 1829.

Syn. *Spiroptera megalostoma* Duj., 1845.

*Ph. alata* Stoss., 1889.

Head naked, with large and simple mouth. Caudal extremity of male with alæ up to its tip; female straight, with rounded extremity.

Host: *Falco nisus*. Proventriculus. Greifsw.

This species is considered by Molin (1860) and Stossich (1889) to be the same as *Ph. alata* Rud.

(70) *PHYSALOPTERA INFLATA* (Mol., 1860), Stossich, 1889.

Syn. *Spiroptera inflata* Mol., 1860.

Length of female 7 mm.; male unknown.

Body striated and attenuated posteriorly. Cuticle of head inflated; no internal teeth on lips. Caudal extremity conical, with an obtuse apex. Vulva in anterior part of body.

Host: *Falco unicinctus*. Stomach and Œsophagus. Brazil.

(71) *PHYSALOPTERA CRASSA* v. Linstow, 1879.

Male 14 mm. long by 1.5 mm. thick; female 23 mm. long by 2 mm. thick.

Lips pyramid-shaped, each with two outer papillæ and two median teeth, of which the inner is tripartite. Œsophagus  $1/4.7$  of body-length. Cervical papillæ .6 mm. from anterior end, situated dorsally and ventrally.

Tail of male rounded,  $1/11.7$  of body-length. Bursa with six pairs of papillæ, of which the anterior five are stalked and arranged in a longitudinal row close to the anus; the 6th and unstalked papillæ are found on the inner side of the 5th pair. Cirri unequal, .66 and .36 mm. long.

Tail of female rounded,  $1/22$ nd of body-length. Eggs  $49\ \mu$  by  $26\ \mu$ .

Host: *Alanda arvensis*. Intestine. Stuttgart.

## (72) PHYSALOPTERA TRUNCATA Schneider, 1866.

Male 25 mm. and female 33 mm. long.

Outer tooth knobbed, "mit beilartiger Schneide." Inner teeth heart-shaped.

Four pairs of lateral and stalked papillæ on male tail; the distance between the 2nd and 3rd somewhat greater than that between the 1st and 2nd, and between the 3rd and 4th. Three pre-anal papillæ in a row, the central one of which is small. The 1st and 2nd pairs of post-anal ventral papillæ small and just behind anus; three larger pairs further down. The ratio of the distances between the 2nd and 3rd, the 3rd and 4th, the 4th and 5th, the 5th and the tip of the tail is about as 1 : 1 : 2 : 2.

Host: *Phasianus gallus*. Stomach. Brazil.

## (73) PHYSALOPTERA FUSIFORMIS v. Linstow, 1902.

Male 18 mm. long by 1.38 mm. thick; female 30 mm. long by 1.97 mm. thick.

Two rounded lips, each with three small papillæ on outer edge. Œsophagus of male  $1/3.8$ , of female  $1/5.3$  of body-length; tail of male  $1/23$ rd, of female  $1/20$ th of body-length. Bursa small and heart-shaped; four pairs of lateral stalked papillæ; one pair of sessile papillæ in front of anus and separated from each other; a pair of sessile papillæ just behind anus; an unpaired papilla in middle of tail, and three more pairs behind it and equidistant from each other.

Vulva in anterior half, and divides body into ratio of 13 : 56. Eggs  $81 \times 26 \mu$ .

Host: *Micropogon* sp. Breslau Museum.

## (74) PHYSALOPTERA DENTATA v. Linstow, 1883.

Male 7 mm. and female 12 mm. long and .96 mm. thick.

Two large lips, each with a large terminal outer tooth and spike-like inner tooth. Cervical papillæ .48 mm. from head end. Œsophagus  $1/4.2$ , tail of male  $1/11$ th, of female  $1/25$ th of body-length.

Bursa lanceolate, alæ ornamented with conical tubercles arranged longitudinally; four pairs lateral stalked papillæ, all are pre-anal; one unpaired papilla in front of anus and three pairs behind it; pairs 1 and 2 close together in middle of tail, often fused together; pair 3 at junction of last two tail quarters.

Eggs  $52 \times 43 \mu$ .

Hosts: *Agama sanguinolenta*. Intestine. Turkestan.

*Vipera berus*. ?

*Phrynocephalus auritus*. Mouth and intestine. "

## (75) PHYSALOPTERA BRITANICA Skrjabin, 1916.

Length of immature female 42 mm., breadth 6 mm. Male unknown.

Œsophagus 5·44 mm. long. Cervical papillæ ·6 mm. from anterior end. Tail conically pointed, ·46 mm. long. Narrow alæ on both sides of body.

Vulva 4·25 mm. from head end.

Two large lateral lips, each with large external tooth; on inner face a series of smaller triangular and pointed denticles on either side of median tooth; 10-11 of these on either side, and the 5th and 6th of them, from the external tooth end, are large.

Host: *Agama* sp. Intestine. British East Africa.

(76) *PHYSALOPTERA SONSINOI* v. Linstow, 1895.

Length of male 6·5 mm., of female 6·7 mm. and ·48 mm. thick.

A conical tooth on top of each lip.

Œsophagus of male 1/4·6, of female 1/2·75, tail 1/9·25 in male, and 1/18th in female of body-length.

Male caudal bursa elongate; 4 pairs of circumcloacal stalked papillæ; 3 pre-anal sessile papillæ in a triangle; 2 large and oval just behind anus, and slightly further back 2 smaller and rounded papillæ; in middle of tail 4 papillæ in a transverse row, and further back 2 pairs, of which the anterior pair is large, and each papilla of which contains 2 pulps.

Right spicule 1·89 mm. long; left spicule ·32 mm. long and much broader.

Vulva divides body into ratio of 5:31. Eggs  $57 \times 39 \mu$ .

Host: *Agama mutabilis*. Stomach. Pisa.

Since the spicules are so unequal, it is possible that von Linstow has mistaken the right for the left.

(77) *PHYSALOPTERA ALOISII-SABAUDIÆ* Parona, 1907.

Male 6 mm., female 11 mm. long.

Body attenuated in anterior third. Two large lips with large tooth, and with a series of denticles and one papilla on each lip. Œsophagus 1/4th of body-length.

Male bursa lanceolate; without tubercles on its surface. Anus surrounded by papillæ; four lateral papillæ longly pedunculate; 2nd and 3rd post-anal pair slightly stalked. Spicules large, long, and unequal.

Female with short tail; eggs oval, small, thick-shelled, and embryonated.

Host: *Agama atricollis*. Intestine. Africa.

(78) *PHYSALOPTERA SPIRALIS* Schneider, 1866.

Length of male 14-22 mm.; length of female 29-67 mm.

Outer tooth pointed, inner tooth absent. Inner face of lips provided with denticles. A pair of these behind the tooth in the middle of the lip; on either side of it an additional pair towards the edge of the lips; dorsally and ventrally a row of about five.

Tail of male straight. Four pairs of lateral stalked papillæ; a pair of sessile papillæ in front of anus and 3 pairs post-anal: of these latter the last pair is situated at about the junction of the last tail thirds, and the other two pairs are situated close together just in front of the middle of the tail.

In the largest females the vulva is 10 mm. from the anterior end. Posterior part of body spirally coiled and tail slightly bent dorsalwards.

Host: *Amphisbæna* sp. Stomach. Brazil.

(79) PHYSALOPTERA ANTARCTICA v. Linstow, 1899.

Length of male 27 mm. by .79 mm. thick; female 42 mm. long by 1.18 mm. broad.

Two lateral lips, somewhat rounded; each bears a conical outer tooth and two small inner side teeth.

Œsophagus of male  $1/8.3$ , of female  $1/8.6$  of body-length; tail of male  $1/23$ rd, of female  $1/54$ th of body-length. Male cloacal aperture large and rounded, and on either side of it four papillæ with long stalks. Thirteen ventral papillæ, of which 3 are pre-anal, 4 just behind the anus in two rows, 2 on either side behind each other in middle of tail, and further back another one on either side.

Tail of female conical, with rounded tip; eggs very thick-shelled,  $54-44 \times 42-31 \mu$ .

Hosts: *Acanthophis antarctica*. S. Australia.

*Cyclodus occipitalis*. Œsophagus. S. Australia.

I have identified this species with my specimens from *Varanus varius* and *Python spilotes*.

(80) PHYSALOPTERA ALBA Stossich, 1902.

Male 25-28 mm. long; female 42 mm. long.

Weakly-developed lips, each with two large submedian papillæ and with very weak teeth.

Male bursa lanceolate, with minute ornamentations on its ventral surface. Four pairs of lateral papillæ with long peduncles. Five pairs of ventral papillæ arranged in two groups, viz. three pairs towards the end of the tail and two pairs just behind the anus, of which the outer pair has double pulps.

Tail of female conical. Vulva at the anterior third of the body. Eggs embryonated, elliptical, with very thick shell.

I have identified this species with *Ph. antarctica* v. Linst., 1899.

Host: *Cyclodus boddaertii*. Proventriculus. Nuova Olanda.

(81) PHYSALOPTERA AMPHIBIA v. Linstow, 1899.

Male 12 mm., female 18 mm. long by 1.05 mm. broad.

Two half-rounded lips. External tooth large and cone-shaped, internal tooth small and tripartite. Œsophagus  $1/4.4$  in the male and  $1/8.3$  in the female of the body-length.



Tail of male  $1/15.5$ , of female  $1/82$ nd of body-length. Bursa with four pairs of stalked lateral papillæ arranged in two groups separated from each other; 1st group of two papillæ is pre-anal, 2nd group is post-anal. Four pairs of ventral sessile papillæ, of which one pair is pre-anal and the other three are in the posterior half of the tail; the central pair of these last three pairs is slightly nearer the front than the hind pair.

Eggs  $55 \mu \times 29 \mu$ .

Host: *Rana macrodon*. Œsophagus and ventriculus. Luzon.

#### SPECIES INQUIRENDÆ.

##### (82) *PHYSALOPTERA ABJECTA* Leidy, 1856.

Length of female .83 inches, breadth .04 inches (10 lines  $\times$  .5 of a line). Male unknown.

"Body most narrowed anteriorly, incurved. Mouth distinctly bilabiate; lips lateral, prominent. Caudal extremity incurved, obtusely conical."

Host: *Psammodiplosis flagelliformis*. Stomach. [U.S.A.]

##### (83) *PHYSALOPTERA BREVICAUDA* v. Linstow, 1909.

Two lips widened outwardly, their pulp narrower at its base; a papillæ in their middle, and right and left of it a cone-shaped tooth.

Male 27 mm. long  $\times$  .83 mm. thick; female 42 mm. long  $\times$  .95 mm. thick. Tail of male rounded,  $1/69$ th of body-length.

Bursa somewhat heart-shaped and alæ ornamented with longitudinal striæ. Six pairs of stalked papillæ—4 pre-anal and 2 post-anal; the post-anal pairs are situated in a transverse row just behind the anus. Spicules equal, 1.4 mm. long, and rounded at their tips.

Vulva just behind middle of body; it divides body into ratio 23:21. Eggs  $39 \times 26 \mu$ .

Host: *Francoelinus adspersus*. Intestine. S.W. Africa.

The shape of the lips, arrangement of the male caudal papillæ, length of the right spicule, position of the vulva, and small size of the eggs, seem to indicate that this species is not a Physaloptera. From the description I am not able to place it in any known genus, and consequently list it under Sp. Inq.

##### (84) *PHYSALOPTERA MALLEUS* v. Linstow, 1883.

Length of male 20 mm. by .76 mm. thick; length of female 42 mm. by 1.5 mm. thick.

Two very large and rounded lips. Œsophagus  $1/6.5$ , tail of male  $1/33.3$ , of female  $1/269$ th of body-length. Bursa oval, with rounded prominences arranged in transverse rows. Six pairs of stalked papillæ, of which 4 pairs are pre-anal, and 2 pairs are



post-anal in position; these last situated just in front of middle of tail. Spicules unequal, the larger having a double barb at its tip. Eggs double-shelled, the outer being the thicker; they are  $46 \times 29 \mu$ .

Host: *Corvus cornix*. Turkestan.

This is probably not a Physaloptera, as evidenced by the rounded lips without teeth, the arrangement of the bursal papillæ, and the presence of a hook on the spicule.

(85) PHYSALOPTERA PAPILLORADIATA v. Linstow, 1899.

Length of male 32 mm., of female 56 mm. by  $790 \mu$  thick.

Two rounded lips.

Œsophagus  $1/12$ th, tail of male  $1/7$ th, of female  $1/127$ th of body-length.

Bursa with 4 pairs pre-anal and 2 pairs post-anal stalked papillæ; 7 pairs of post-anal ventral papillæ, of which 1 pair is just posterior to the anus, and the remaining 6 pairs are aggregated at the posterior end of the tail.

Eggs  $26 \times 12 \mu$ .

Host: *Canis lupus*. Pectoral cavity. Persia.

As figured by von Linstow, the arrangement of the caudal papillæ is very similar to that of *Ph. rotundata* v. Linst., except that in *rotundata* there are 5 papillæ at the base of the tail, whereas in *papilloradiata* there are 12. I have placed this species under Sp. Inq. because of this similarity, and because Seurat has found *Ph. rotundata* to be a Habronema.

(86) PHYSALOPTERA SPIRULA Hempr. & Ehrenb., 1828.

Male 6 mm. long; female unknown. Head continuous with body. Mouth papillate. Caudal extremity of body provided with closed bursal alæ.

Hosts: *Procavia syriaca*. } Large intestine. Syria and Arabia.  
*Procavia capensis*. }

(Extracted from Hall, 1916.)

SPECIES WRONGLY ATTRIBUTED TO THE GENUS.

(87) PHYSALOPTERA ROTUNDATA v. Linstow, 1906.

Length of male 15.6 mm. by 1.1 mm. thick; length of female 20.3 mm. by 1.5 mm. thick. Both ends of body rounded.

Two large lips, each bearing a prominent papilla on each side. Œsophagus  $1/8.6$  in male,  $1/9$ th in female, tail in male  $1/40$ th, in female  $1/20$ th of body-length.

Bursa narrow, with 6 pairs of lateral stalked papillæ, of which 4 pairs are pre-anal and 2 pairs post-anal. Two pairs of ventral papillæ at tip of tail, and just in front of them an unpaired papilla. Spicules unequal; right  $510 \mu$ , left  $2170 \mu$  long, both with rounded tips.

Vulva divides body into ratio of 6:15. Eggs  $39 \times 26 \mu$ .  
 Host: *Otis houbara*. Intestine. Koenigsberg.  
 Seurat (1914 d) has identified this species as a *Habronema*.

(88) *PHYSALOPTERA BULBOSA* v. Linstow, 1906.

Host: *Pavo spicifer*. Stomach.

I have recently found specimens of this parasite in the proventriculus of *Pavo cristatus* from India. From my observations on this material I find that this parasite is not a *Physaloptera*, but belongs to the genus *Cyrnea* Seurat, 1914. A detailed description of it will appear in a later publication.

(89) *PHYSALOPTERA CONTORTA* Leidy, 1856.

"Body capillary, most narrowed anteriorly with the posterior 4/5th spirally contorted; white, with the intestine brown. Lips prominent, constricted from the body, trilobate. Tail short conical, acute, in the male with narrow alæ each furnished with, five funnel-shaped pores. Length of female from 6 lines to an inch; breadth to one quarter of a line; male from one-half to three-quarters of the size."

Hosts: *Emys serrata*, *Emys reticulata*, *Cistudo carolina*, and *Kinosternum pennsylvanicum*. Stomach. [U.S.A.]

Baylis and Lane (1920) suggest that this species is probably identical with or closely related to *Spiroxys contorta* (Rud., 1819), Schn., 1866. I have been able to examine some specimens of *Spiroxys contorta* obtained from *Emys orbicularis*, and from my observations Baylis and Lane's view appears justifiable. According to Leidy's description, these parasites must be excluded from the genus *Physaloptera* because of their trilobed lips. Molin (1860) has already doubted the *Physalopteran* affinities of this species.

(90) *PHYSALOPTERA CONSTRICTA* Leidy, 1856.

Length, female  $1\frac{3}{4}$  inches, male half as long.

Lips large, lateral, constricted from body, and trilobate. Tail of male with long and narrow turgid alæ; that of the female incurved, conical, and acute.

Host: *Tropidonotus sipedon*. Stomach. [U.S.A.]

The nature of the lips definitely excludes this parasite from the genus *Physaloptera*, no members of it having trilobed lips. Baylis and Lane (1920) suggest that this parasite may be a *Tanqua*. I agree with them in so far that it falls into the family *Gnathostomidae* as redefined by them, but as to its closer relationship to any of the genera of this family, it does not appear justifiable to draw any conclusions; Leidy's brief description of the parasite is equally applicable to the genus *Spiroxys* as to the genus *Tanqua*.

Molin (1860) also expressed doubt as to this species belonging to the genus *Physaloptera*.

## (91) PHYSALOPTERA MUCRONATA Diesing, 1851.

Host: *Alligator mississippiensis*. Georgia.

This parasite has been found by Molin to be an Ascarid, and von Drasche has identified it with *Ascaris lanceolata* Mol., 1860.

## (92) PHYSALOPTERA OVATA v. Linstow, 1907.

Length of male 13.8 mm.; length of female 16.8 mm. by 1.22 mm. thick.

Mouth surrounded by 6 cones. Œsophagus of male 1/4.4, of female 1/3.5, tail of male 1/14th, of female 1/53rd of body-length.

Bursa oval, with 5 pairs of equidistant and lateral stalked papillæ, the 2nd being the longest; 2 pairs are pre-anal. Spicules equal 290  $\mu$  long.

The vulva divides the body into the ratio of 13:31. Eggs narrow,  $42 \times 13 \mu$ .

Host: *Astur melanoleucus*. Ventriculus. Cameroon (Kamerun).

The nature of the lips rules this species out of the genus *Physaloptera*; this is supported by the nature of the bursal papillæ and by the extremely narrow egg.

The description is too incomplete to definitely say to which genus it should be transferred, but it appears to have some resemblance to the genus *Cyrnea* Seurat, 1914.

## (93) PHYSALOPTERA SAGINATA Rud., 1819.

Syn. *Spiroptera saginata* (Rud.), Duj., 1845.

I examined examples of this species from *Corvus cajanus* and *Caprimulgus guianensis* while at Vienna, and am consequently able to confirm Molin's (1860) view that this species is a *Spiroptera*.

## (94) PHYSALOPTERA STRIATA v. Linstow, 1883.

Length of male 18 mm., breadth .48 mm.; length of female 25 mm., breadth .66 mm.

Two dorso-ventral lips, small and rectangular, having a wavy anterior border and divided into three parts internally; 4 small interlabia. Tail of male spirally rolled, 1/37.5 of body-length; tail of female rounded, 1/83rd of body-length.

Caudal alæ of male with longitudinal striations. Four pairs of pre-anal stalked papillæ; 1 unpaired papilla in front of anus; 2 pairs post-anal and dividing tail roughly into thirds.

Vulva divides body into ratio of 3:2. Eggs  $46 \times 25 \mu$ .

Hosts: *Tropidonotus hydrus*. Turkestan.

*Ciconia alba*. Stomach. Turkestan.

Seurat has obtained a *Cyrnea* from different species of *Ciconia*, which he identifies with *Ph. striata*. This species is undoubtedly not a *Physaloptera*, and from von Linstow's figure and description of the lips I think Seurat is correct in transferring it to his genus.

(95) *PHYSALOPTERA STRONGYLINA* Rud., 1819.Syn. *Spiroptera affinis* Duj., 1845.

Length of male 7·87 mm., of female 15·25 mm. to 20·25 mm.

Body white and head appears to have papillæ; tail of male with lateral alæ, so that it resembles a Strongylid tail. Spicules fairly long and thick.

Host: *Cuculus seniculus*. Stomach and intestine. Brazil.Molin ruled this species out of the genus *Physaloptera*, stating that it belonged to a new genus.

The description is too incomplete to warrant it being referred to any now known Nematode genus.

(96) *PHYSALOPTERA TENUICOLLIS* Rud., 1819.Syn. *Spiroptera tenuicollis* (Rud.), Duj., 1845.

Male unknown; length of female 41 mm., breadth 1·15 mm.

Mouth rounded; anterior end sharply attenuated for a distance of 2·25 mm.

Host: *Falco haliæetus*. Intestine.

Molin (1860) has identified this species as an Ascaris.

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49. The Oligochaeta of the Oxford University Spitsbergen Expedition. By J. STEPHENSON, M.B., D.Sc., Lecturer in Zoology, Edinburgh University.

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(Text-figures 1-6.)

(Results of the Oxford University Expedition to Spitsbergen,  
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INTRODUCTION.

The Oligochaeta obtained by the Oxford University Spitsbergen Expedition were contained in fifteen tubes—four from Bear Island and the remainder from Spitsbergen. The specimens from Bear Island belonged to two species—*Enchytræus albidus* Henle and *Nais josinæ* Vejd.,—both well known. Of those from Spitsbergen, a number were sexually immature and therefore indeterminable (*Mesenchytræus* sp., two species of *Henlea*, *Enchytræus* sp.); the remainder, most of which occur in more than one of the tubes, comprise two species of *Henlea*, one of *Enchytræus*, and two of *Lumbricillus*, all apparently new. With the exception of the *Nais* from Bear Island, all the worms thus belong to the family Enchytræidæ.

Our previous knowledge of the Oligochæta of Spitsbergen and Bear Island is due almost entirely to Ude (17), who, in addition to collections from Bear Island (then examined for the first time), had also at his disposal a small collection from Spitsbergen, sent to him by Michaelsen and tentatively named, the names having already been entered in the 'Tierreich' volume on Oligochæta (11).

The following species are all that have been recorded:—

From Spitsbergen:—

*Lumbricillus pagenstecheri* (Ratz.) (originally determined and entered in the Tierreich volume as *L. nervosus* (Eisen)).

*Fridericia leydigi* (Vejd.).

*Mesenchytræus* sp. indeterminable.

From Bear Island:—

*Marionina ebudensis* (Clap.).

*Lumbricillus fossarum* (Tauber).

*Lumbricillus henkingi* Ude.

*Enchytræus albidus* Henle.

The only one of these collected by the Oxford Expedition is *Enchytræus albidus*. All, as will be seen, belong to the Enchytræidæ.

The Enchytræidæ have always furnished the great majority of Oligochæta from high latitudes, and there exists a considerable number of records of species of the family from Nova Zembla, Northern Siberia, North Russia and Norway, Greenland, Arctic Canada, and Alaska—especially species of the genera *Henlea* and *Mesenchytræus*. Welch has in recent years (20, 21, 22) drawn attention to previous records of Enchytræidæ found actually on ice and snow, and has himself examined and described a number of species from high latitudes, and from snowfields and glaciers. Some of these worms show a resistance to cold that can only be described as marvellous. *Mesenchytræus gelidus* was found "abundantly on the snowfields"; it "also occurred on the snow on the mountain slope in a dense forest of fir and hemlock," and "on the snow below the ice front and outside of the lateral moraines of the Nisqually glacier; . . . when placed on hard-packed snow during their active period, they are able to bore down through it at will; . . . the snow on which they are found is not permanent through the entire season, but melts with the coming of summer, and it therefore appears that a part of their life-history must be spent on or in the ground." *Mesenchytræus solifugus* var. *rainierensis* was "abundant on the higher snowfields and glaciers of Mt. Rainier in early summer; it was found on snowfields which seldom thaw during the summer, and they evidently pass the entire existence, generation after generation, in the snow and ice." Beddard (1) mentions that an Enchytræid has been found frozen in a block of ice, and recovered. Mr. Elton writes that he has subjected the worms which I have named *Enchytræus crymodes* to an experiment in which they were frozen solid and that they survived.



It was thus to be expected that Enchytræids should constitute the bulk of the collection. There is no mention of snow in the data relating to the worms; and since they thus pass at least a part of their life on or in ground free from snow, the conditions under which they live are those of Welch's *Enchytræus gelidus* rather than of *M. solifugus* var. *rainierensis*.

### ZOOGEOGRAPHICAL RELATIONS.

The Oligochaeta may be divided, with reference to their habitat, into limnic, littoral, and terrestrial forms; and the Oligochaeta of Bear Island and Spitsbergen may be classified under these headings as follows:—

LIMNIC.	LITTORAL.	TERRESTRIAL.
<i>Nais josinae</i> .	<i>Lumbricillus necrophagus</i> .	<i>Henlea brucei</i> .
<i>Henlea heleotrophus</i> .	<i>Lumbricillus agialites</i> .	<i>Enchytræus albidus</i> .
<i>Henlea</i> spp. (2).	<i>Lumbricillus fossarum</i> .	<i>Fridericia leydigi</i> .
<i>Enchytræus crymodes</i> .	<i>Lumbricillus henkingi</i> .	<i>Mesenchytræus</i> sp.
<i>Mesenchytræus</i> sp.	<i>Lumbricillus pagenstecheri</i> .	
	<i>Marionina ebudensis</i> .	
	<i>Enchytræus albidus</i> .	
	<i>Enchytræus crymodes</i> .	

There is no record of the habitat of some of the previously recorded species: of *Lumbricillus fossarum*, which, however, is elsewhere found on the shore, and is therefore so entered here; of *Enchytræus albidus* recorded from Bear Island by Ude, which is also entered as littoral, since all his specimens from Bear Island of which the habitat is recorded were littoral, and the worm is elsewhere common on the shore; and of *Fridericia leydigi*, which is entered as terrestrial, since most of the *Fridericias* are so.

All the smaller Oligochaeta, and therefore all the forms which are represented in the present and former collections from Spitsbergen and Bear Island, are easily transported, and hence are of only slight value for considerations of zoogeography. Limnic forms have a great diversity of means of dispersal; they may spread directly throughout a river system—though this, of course, has no bearing on the present enquiry; their cocoons are easily transported in the mud which adheres to the feet of wading birds; some forms are known to encyst, and hence may be transported by birds even in the adult state. As a consequence of this easy distribution, the same genera—sometimes even the same species—are found in widely distant places; the case is similar to that of the Rotifera and Protozoa, of which the same genera and species are found in ponds and streams all over the world. To illustrate by means of an example, there appears to be but one genus, *Branchiodrilus*, of limnic Oligochaeta which is peculiar to India, while a number of species are found both in India and England, or India and Europe (species of *Nais*, *Chaetogaster*, *Dero*, *Aulophorus*, *Pristina*, etc.).

Littoral forms, living on the shore and exposed at times to immersion in salt water, have additional means of dispersal. Being, unlike Oligochætæ in general, immune to salt water, they can be transported in masses of seaweed; or more commonly their cocoons are so transported, entangled in masses of weed or other detritus. Not only can they take possession of a whole coast, and spread along the shore-line, but they may in this way travel over sea for long distances. *Pontodrilus*, for example, which occurs along the coasts of India, has a circummundane distribution.

Even terrestrial Oligochætæ are by no means always dependent on their own unaided activities for enlarging their distribution; there are a considerable number which are especially liable to be transported accidentally—by man or other agencies,—and which show an especial capacity for establishing themselves where they happen to be deposited. The smaller the worms the easier is their dispersal; certain small species of earthworms of the genus *Dichogaster*, which has its proper home in Africa, have spread all round the warmer regions of the globe.

Few, however, possibly none, of the worms of Spitsbergen and Bear Island are exclusively terrestrial. Of those given as terrestrial in the above table, *Enchytræus albidus* is often found on the shore; it is perhaps the most widely distributed of all Enchytræids, and occurs all over Europe, in North America, and in South America as far as Patagonia and Tierra del Fuego, as well as within the Arctic circle in Greenland and Nova Zembla. The species of *Mesenchytræus* found at Cape Boheman among plants in dry tundra was also obtained among mosses on the banks of a freshwater pond, more or less under water, and is therefore limnic as well as terrestrial. The *Henlea* found among *Dryas* etc. on a hill near the coast of Freshwater Bay was also found in the Bruce City region, possibly in a limnic or littoral habitat (details of habitat are wanting for this tube). *Fridericia leydigi*, previously obtained from Spitsbergen, is probably the most strictly terrestrial of all the above species, occurring elsewhere in earth rich in humus and under moss.

There can thus be no question of anything peculiar in the Oligochæte fauna of Spitsbergen and Bear Island. All the genera are easily transported, and all (except perhaps the Naidid genus *Nais*) have previously been found within the Arctic circle—*Henlea* in Nova Zembla, N. Siberia, N. Russia, N. Norway, and in the Canadian Arctic; *Enchytræus* in N. Russia, Greenland, and the Canadian Arctic; *Lumbricillus* in Nova Zembla, N. Siberia, the Canadian Arctic, and Greenland; *Fridericia* in Nova Zembla, N. Russia, and N. Siberia. All these genera also occur in Alaska.

As to whether particular species of Spitsbergen Oligochætæ have been evolved locally, or imported, it is as yet impossible to say, until neighbouring lands have been more thoroughly explored. There is some slight ground for supposing that some, at least, may have been evolved on the island. On the whole, no

doubt, it is the commoner species of the neighbouring lands that are already known to us; and on the whole, no doubt, it is the commoner species that, from their frequency, have most chance of being transported. If it had been throughout a case of simple transportation, therefore, we might have expected to find that a larger number of the species of worms were known from elsewhere also.

It seems hazardous to suppose that any of the present Oligochaete fauna could be descended from ancestors existing in Spitsbergen before the glacial period. It is true that we now know species which can live their lives through, and reproduce themselves, on ice and snow. The food of such worms, according to Welch, writing of the specimens from Mt. Rainier, seemed in one case (*Mesenchytræus gelidus*) to be microscopic algæ having the appearance of *Pleurococcus*, and the snow over which the worms were crawling had a red colour due to a minute unicellular plant; in the case of the other worm (*M. solifugus* var. *rainierensis*) the food could not be determined.

But the food-supply of glacier and snow worms must, one would say, be precarious: and it seems dangerous to assume its unfailing presence throughout the long duration of the glacial period.

On the other hand, there are apparently no facts which seem to contradict "the most reasonable hypothesis of the origin of the present fauna—namely, an 'accidental' peopling since the period of maximum glaciation, during which time Spitsbergen has been as widely separated from adjacent lands as it is now."

#### ON THE "PEPTONEPHRIDIA" OF THE ENCHYTRÆIDÆ.

Certain structures connected with the first portion of the alimentary canal in a number of Enchytræids are known as "peptonephridia," or sometimes as "salivary glands."

(1) The best known of these structures are a pair of tubules which arise from just behind the pharynx, and extend backwards for some little distance free in the body-cavity. They are well developed, for example, in *Enchytræus albidus*, a worm which is abundantly represented in the present collection. Here the tubules open into a dorsal diverticulum of the alimentary canal just behind the pharyngeal mass: they sometimes extend backwards into segm. v., while sometimes they do not transgress the hinder limit of segm. iv.; their general course is sinuous or contorted, and in addition the outline of the walls is marked by numerous smaller sinuosities or crenations. The diameter of the tubules varies—it may be about  $50\mu$ , or may be less; that of the lumen may be  $42\mu$  or less; the diameter is least near the origin of the tube from the alimentary canal, where the whole structure is only  $16\mu$  thick, and the lumen is very small. The walls are mostly thin, about  $4\mu$  thick, but in places are much thicker—as much as  $15\mu$ ; numerous nuclei are seen in the walls—in a transverse section of one of the tubes there may be about six, *i. e.* the lumen is intercellular.

(2) In the genus *Henlea* there are often found other organs, situated in the middle line, one dorsally and one ventrally on the œsophagus, in segm. vi., sometimes extending forwards into v., and backwards behind vi. for, it may be, several segments. The association with the wall of the alimentary tube is here much more intimate than in the case of the former structures; these are closely apposed to the wall of the œsophagus for the whole or the greater part of their extent; they may even be contained for a considerable part of their extent within the wall, between the epithelial and muscular coats (Welch, in *H. moderata* (19), which I can confirm in *H. brucei* and *H. heletrophus*). They frequently give branches.

While the former structures have little about them that can remind the observer of nephridia, these have much more the appearance of the peculiar type of nephridium found in the Enchytræidæ—a spongy-looking, scarcely staining tissue, with nuclei but no visible cell-limits; sometimes there seems to be no lumen in the interior—nothing more than the interstices of the spongy cell-substance, sometimes there are irregular spaces and tubular cavities, and sometimes a single well-defined central lumen. They have, however, no ciliated funnel or any kind of internal opening. Cejka, in the worms which he called *Hepatogaster*, states (3) that there are indications of the double origin of these apparently single and median structures; in this I agree (compare the transverse section of a ventral organ of *H. brucei*, fig. 1; the description of the ventral organ in *Henlea* sp. (1), *post.*, and of the dorsal organ in *H. heletrophus*, where possibly there is no connection between the masses on the right and left sides); while Welch finds that in *H. ochracea* (22) the organs are actually paired, one pair dorsally and one pair ventrally. It is, perhaps, this type of gland which is intended by Friend in his reference to the salivary glands of *H. alba* (7) and *H. inusitata* (8), and to the “special glands” of *H. bisetosa* (8).

(3) There is a third type of organ, which is apparently widely spread in the family. Descriptions of these structures are given for all the newly described species below, and they also occur in the *Mesenchytræus*; I have described and illustrated similar structures in the Indian worms *Enchytræus barkudensis* (14, and see also pl. vi. fig. 1 in 15) and in *Fridericia carmichaeli* (15). Briefly, these organs consist of a pair of rounded, or ovoid and bulb-like, masses of cells, solid, situated behind the pharyngeal mass on the dorsal side of the alimentary tube, and connected with the tube by a stalk, which is at any rate partly solid, but is usually hollow in its proximal portion—*i.e.*, the cavity of the alimentary tube may penetrate the basal portion of the stalk. Ude probably had this type of organ before him when he described the rudimentary salivary glands of *Bryodrilus ehlersi* (16), two small pear-shaped bodies, in which no lumen could be recognized immediately behind the pharynx; and, indeed, since I first met with these structures some years ago, I believe I have myself



conceived them as a rudimentary kind of organs of the first type.

Whether all these structures should go by the same name—whether they are all modifications of one original structure—seems doubtful. Those of the second type are quite possibly nephridia. It will be remembered that the Euchytræids have, as a rule, no nephridia in the first six segments (Bretscher (2) has established a separate genus for a worm in which the first nephridium occurs in segm. iii., the funnel being in ii.); and the occurrence of dorsal and ventral “peptonephridia” in segm. vi., extending thence, it may be, forwards or backwards, or both forwards and backwards, their obviously similar constitution, and their fundamentally paired nature would seem to justify the assumption that they are really the nephridia of segm. vi. which have become associated with the œsophagus. If, however, we look on both dorsal and ventral organs as fundamentally paired (as we seem justified in doing, *v. ant.*), we should then have two pairs of nephridia belonging to segm. vi. In *H. brucei*, in addition to dorsal and ventral “peptonephridia” in segm. vi., there are also in the same segment—indeed in the same section—a pair of ordinary nephridia (the first nephridium being here in segm. vi. with the funnel in v.), i. e., *three* pairs in the one segment.

Whether the organs discharge an excretory substance into the œsophagus, or a digestive juice—or, indeed, whether they discharge anything at all,—is doubtful. Cejka says that the openings are always hard to find in sections; from which phraseology it would seem doubtful whether they actually have definite mouths; Welch does not mention any openings, nor have I found any in my preparations. On the whole, they are perhaps more likely to be excretory, since they have an intimate relation to the blood-spaces (in *H. leptodera* they run in the œsophageal sinus and are directly bathed by the blood (Cejka, 4); in *Hepatogaster* also they are bathed by the blood in the sinus, which may penetrate between the individual cells; I have found the same conditions, *v. inf.*).

But the nephridial nature of the first group of organs, which have for long passed under the name of “peptonephridia”—the sinuous or coiled tubes which extend back, from the pharynx, free in the cœlom—seems doubtful. These do not show the peculiar structure of the Euchytræid nephridium; they have no internal opening; indeed, the only feature that is brought forward to substantiate their nephridial nature is the intracellular lumen. But in *Enchytræus albidus* (*v. ant.*) the lumen is certainly not intracellular. And in any case there is no fundamental difference between intercellular and intracellular tubes; whether the lumen of any tube is intracellular or not depends on the size of the lumen and the size of the cells of which the tube is composed. Suppose we start with a tube of fair size, in the cross-section of which several cells are seen to bound the lumen; if the size of the tube is diminished, fewer cells will serve to surround the cavity,



and fewer will be seen in any transverse section. Still diminishing the width of the lumen, two cells, and finally one single cell, will go all round the lumen—*i. e.*, only one cell will be seen in any given transverse section of the tube, and the lumen will be described as intracellular. There is thus really no reason for assuming the nephridial nature of these tubules of the *Enchytræidæ*, and in my opinion they should not be called nephridia.

The third group of structures—the bulb-like organs—are even more unlike nephridia; nor, except for their assumed connection with the tubular organs first described, could it ever be supposed that they were nephridial. It is possible that they are, as has been suggested, vestigial remains of the tubules; they are connected to the same dorsal diverticulum of the alimentary canal as these. In *Enchytræus albidus*, however, I find, along with the typical tubules, and just in front of and lying against the narrow proximal part of these, rather indefinite groups of cells somewhat similar to the bulb-like organs. To establish the homology of the bulb-like organs with the tubules it would be necessary to ascertain definitely whether they do or do not occur along with these, and whether or not intermediate forms exist.

The second group of organs, then—the dorsal and ventral “peptonephridia” of the genus *Henlea*,—may provisionally be taken to be nephridia. But there is no evidence whatever of their digestive function, and I propose for them the name *œsophageal nephridia*.

The first group—the sinuous tubules—are quite possibly not nephridia at all. Since the alternative name *salivary glands* has long been in use for them, I would reject the name peptonephridia in favour of this.

The third group—the solid bulb-like organs—do not seem to be nephridial, and their function, if they have one, is quite unknown. I propose a purely descriptive term, the *postpharyngeal bulbs*, as most suitable for them.

#### THE GENUS *Henlea*.

*Henlea* is a large genus, and contains species showing a wide variety of structure. Characteristic of a number of species are the œsophageal sacs in or about segm. viii.; and the question arises whether the presence or absence of these sacs should not be made the basis of a separation into two genera, or at least subgenera.

This course has already been proposed by Friend (7, 8)—forms with œsophageal diverticula to be called *Henlea*, those without to receive the name *Henleanella*. In the second of the papers just referred to, Friend remarks that it would be advisable to make a third group for those species in which the alimentary tube dilates gradually to form the intestine. In a subsequent paper (9), Friend proposes a different criterion for the third group, *viz.*, the origin of the dorsal vessel in the region of the clitellum (in most

species the dorsal vessel arises considerably in front of the clitellum); this third group to be called *Henleana*. These divisions are apparently conceived as subgenera (certainly so in the first two papers).

Friend's suggestion as regards the œsophageal diverticula seems particularly useful. But it is illogical and inconvenient to have a double or triple principle for the simultaneous division of a group; the subgroups will not be mutually exclusive. What, for example, would become of a form with both œsophageal diverticula and a posterior origin of the dorsal vessel—at the same time a *Henlea* and a *Henleana*; or, for that matter, of one with a posterior origin of the dorsal vessel and no diverticula—both a *Henleana* and a *Henleanella*?

In 1910 Cejka (3) established a genus *Hepatogaster* for two species which are obviously nearly related to *Henlea*, the chief distinctive characters being the gradual dilatation of the œsophagus to form the intestine, the presence of a mass of tubules closely surrounding the alimentary tube in segm. viii., and of characteristic longitudinal canals in the epithelium of the hinder end of the digestive tract. The value of the first distinction is doubtful, e. g. in *Henlea heleotrophus* I am not certain whether or not the intestine can be said to arise as a sudden dilatation of the alimentary tube; at first I thought not, but later I altered this in my notes by adding the words "this might be called a sudden widening, and so would agree with the diagnosis of *Henlea*." The second of Cejka's points of distinction occurs also in *Henlea tubulifera* Welch and *H. moderata* Welch; while, as Welch remarks (23), the value of the third distinction as a generic character remains to be demonstrated. Welch retains the genus, though with some doubt. Delphy (5) also considers it as distinct.

The œsophageal diverticula of *Henlea*, when present, may have walls which are fairly smooth and even, or which are variously folded; and I regard the "tubuliferous" condition of *H. tubulifera*, etc., and of *Hepatogaster*, as simply a higher degree of this folding, followed by fusion between the adjacent folds and between the two sacs above and below the alimentary tube. An intermediate condition is that of *H. nasuta* as described by Michaelsen (10, cf. especially pl. fig. 1), where the folding of the walls is very considerable, and there is only a very small central free space, but the two sacs are not fused above and below the œsophagus. The difference between *Henlea* and *Hepatogaster* seems, in fact, to be less than that between *Henleanella* without sacs and *Henlea* with them.

For the present, then, I would retain the genus *Henlea*, but I would recognize three subgenera:—

- (1) *Henleanella*, with no œsophageal diverticula.
- (2) *Henlea*, with œsophageal sacs.
- (3) *Hepatogaster*, with a mass of tubules surrounding the alimentary tube and taking the place of the sacs.

I would disregard the sudden or gradual widening of the tube

in these subgeneric distinctions; but it is possible that a posterior origin of the dorsal vessel will be a sufficient ground for removing out of the genus altogether the forms in which it occurs.

ON THE RELATIONS OF THE GENERA *Lumbricillus* AND  
*Enchytræus*.

I have previously (13) pointed out the close relationship between the above two genera, and described several species with intermediate characters; *Enchytræus dubius*, which I then placed in the genus *Enchytræus*, I should now assign to *Lumbricillus*. Welch also has some remarks that bear on the subject (19, 23).

The distinguishing characters of the two genera may be said to be (1) the setæ—the distal portion of the shaft being straight in *Enchytræus*, curved, so that the setæ have the usual double (sigmoid) curve, in *Lumbricillus*; (2) the copulatory glands—usually absent in *Enchytræus*, usually present in *Lumbricillus*; (3) the testes, divided in *Lumbricillus*, undivided in *Enchytræus*; and (4) the penial bulb—single, compact, encapsuled, and penetrated by the vas deferens in *Lumbricillus*, represented by discrete groups of cells around the end of the duct in *Enchytræus*. In addition, red blood would be in favour of *Lumbricillus*, colourless blood more in favour of *Enchytræus*.

Of the species described in the present paper, *Lumbricillus ægialites* has the straight setæ of *Enchytræus*, and so has *L. necrophagus*; while *Enchytræus crymodes* has a penial bulb of the lumbricilline type, copulatory glands, and hæmoglobin in the blood. These species thus bear out what I have previously written regarding transitional forms, and render a sharp separation between the genera impossible. Still less is there such a sharp distinction between the two as would justify their position as the representatives of two subfamilies, the Enchytræinæ and Lumbricillinæ, established by Eisen (6).

PERIODS OF SEXUAL MATURITY.

Some of the worms in the collection were sexually mature, others immature. But it is not possible to draw any general conclusions from the data regarding the season of maturity in high latitudes. *Enchytræus albidus* was mature on Bear Island in June and *E. crymodes* in early August in Spitsbergen; but an immature *Enchytræus* was also collected on August 6th. *Henlea heleotrophus* and *H. brucei* were mature in early August—*H. heleotrophus* also as early as July 10th; but other species of *Henlea* were still immature in early August. The two species of *Lumbricillus* were mature towards the end of July and beginning of August; the *Mesenchytræus*, however, was immature at any rate up to the end of July.

# PARASITIZATION.

Finally, I may be allowed to draw attention to the excessive parasitization of most of these worms, which goes much beyond anything that I have previously seen in members of this group. Not only were there numerous parasites, of more than one group of Protozoa, in the alimentary canal, but many of the worms had cysts in the genital region, body-wall, or coelom, in which spores were forming. It seems probable that the frequent structural changes in the alimentary canal, as well as other changes in the contents of the coelom, may be due to this parasitization.

## SYSTEMATIC.

Fam. NAIDIDÆ.

Genus NAIS Müll. em. Vejd.

NAIS JOSINÆ Vejd.

Bear Island; in littoral region of a tarn near Walrus Bay, in the water; 15.vi.1921. A single specimen, non-sexual.

Fam. ENCHYTRÆIDÆ.

Genus HENLEA Mich.

HENLEA (HENLEANELLA) HELEOTROPHUS, sp. n.\*

Spitsbergen; among mosses on the bank of a fresh-water pond, more or less under water, Bruce City. August 1st-8th, 1921.

Spitsbergen, Bruce City region (no data regarding habitat); 10.viii.1921. One specimen from each of these tubes.

Length 8-10 mm.; diameter .4 mm. Segments 40, with a few more not yet differentiated at the hinder end. Colour brownish in the first tube, black in the second (fixed with Bouin). Prostomium bluntly triangular, the triangle being about equilateral. Head-pore between prostomium and first segment. No dorsal pores.

Clitellum on segments xii. and xiii., well marked.

Setæ enchytræine in form (*i. e.*, straight in their distal portion), the tip moderately sharply pointed. In front of the clitellum the ventral bundles have apparently four setæ (not well seen), behind the clitellum 4, 5, 6, and once 7; the lateral bundles have usually five setæ, sometimes 4 or 6, in front of the clitellum, and behind the clitellum 4, 5, 6, once 7, and once 8.

The "taste organ" on the floor of the pharynx is similar to that described for the next species, except that its base of attachment appears to be a little narrower.

\* 'Ελεώτροφος, bred in the marsh.



The septal glands are bulky, the last, in segm. vi., causing septum 6/7 to bulge back very considerably.

Dorsal and ventral œsophageal nephridia are present, but less conspicuous than in the next species. The dorsal nephridium is double, consisting of two masses, one on each side of the middle line, attached behind to the dorsal side of the dorsal vessel near the angle which the vessel makes with the septum (6/7) and laterally to this on the anterior face of the septal gland; the masses have perhaps a small connection with each other across the middle line. Each is very irregular in shape, and the attachment to the dorsal vessel and septal gland is relatively narrow; portions of the mass consist of long strings of cells extending forwards and upwards in the segment.

The ventral nephridium is contained wholly in the œsophageal wall, and is rather indistinct—indeed, in one of my two series of longitudinal sections it is scarcely to be made out; it is not obviously paired, and extends behind into segm. vii.

A pair of postpharyngeal bulbs are present—small solid groups of cells behind the pharyngeal mass, continuous with a dorsal upfolding of the œsophageal epithelium. These structures may be compared with those described in the account of the next species; but here they are very much less definite, the knobs of cells less distinctly limited, the lumen of the upward fold of œsophageal epithelium much less marked, indeed hardly present, and the whole smaller.

Chloragogen cells begin in segm. vii.; in this segment, however, they are only scanty.

The œsophagus expands to form the intestine in segm. viii. In this segment there is a slight invagination backwards of the œsophagus into the broader intestine behind; there are no diverticula. In each of the segments behind vii. the canal is swollen out into an ovoid shape, and this is the case in the genital segments also. There are no chylus-cells.

The cœlomic corpuscles are large, granular, and elliptical, oval, or fusiform in shape, of an average length of  $29\mu$ ; small nuclei, with a central nucleolar dot, are visible in some, though not distinctly discoverable in all.

The dorsal vessel originates in the anterior part of segm. ix. as a sudden swelling just behind the septum; it contains numerous corpuscles. The blood was probably colourless.

The nephridia have a relatively large anteseptal portion in which the central lumen undergoes some windings; the post-septal portion is ovoid, and not large; in one specimen the duct appears to be prolonged back from the hinder end of the body of the organ, and lies on the body-wall; in a second, the duct can be seen in sections to come off from the under (or under and outer) side of the postseptal portion considerably in front of its hinder end.

The sexual organs are more completely developed in the second specimen (taken on the 10th of August), which will therefore be described.



The testes are small, and not lobed. Sperm-morulae and the early stages of spermatozoa are free in segm. xi., but not in large numbers.

The male funnel is small, subspherical in shape,  $108\mu$  in diameter, with spermatozoa clustering round its mouth. The first portion of the vas deferens is of a diameter of  $15\mu$ , but this is only for a very short distance on both sides of the septum, and the main part of the duct forms a very narrow tube  $6\mu$  in diameter, packed tightly in a coil just behind the septum and entirely in front of the level of the male pore. The penial body is of the lumbricillid type, subspherical in shape,  $120\mu$  in diameter, compact, with a definite outline and contained in a definite muscular capsule.

The ovary is small; large ova are contained in segm. xii.

The spermathecal duct is straight for the most part, of some length,  $28\mu$  in diameter, directed downwards and forwards; towards its ental end it bends inwards; there are a few pear-shaped lobules of cells around its ectal end, but these may be peritoneal aggregates and not epithelial gland-cells. The ampulla is only slightly dilated, measuring  $56\mu$  in diameter; the two ampullae are continuous across the middle line—there is not even a narrowing of the lumen to demarcate one from the other. There is no connection between the lumen of the oesophagus and that of the ampullae; the structures do not anywhere come into contact. The length of the conjoined ampullae is  $160\mu$  (computed—it extends through 20 longitudinal sections each of a thickness of  $8\mu$ ).

There are no copulatory (ventral) glands.

The first specimen is altogether smaller than the second, and was collected a little earlier. The diameter of the male funnel is  $75\mu$ ; though here, too, spermatozoa are clustering round the mouth. The penial body is also about  $75\mu$  in diameter. The spermathecal ampulla is no wider than the duct, though the epithelium is much lower and the lumen therefore more capacious; the inner ends of the ampullae are not in contact either with the oesophagus or with each other; there is an interval of about  $16\mu$  between the ampullae of the two sides.

#### HENLEA (HENLEA) BRUCEI, sp. n.

Spitsbergen; dry tundra, among *Dryas*, etc., on hill near coast, Freshwater Bay, Prince Charles Foreland; 10.vii.1921. A single specimen.

Spitsbergen; Bruce City region (no data concerning habitat): 10.viii.1921. A single specimen.

Spitsbergen; among plants growing on shingle of raised beach, Bruce City; 11.viii.1921. Two specimens.

Length 6–8 mm.; diameter  $\cdot 31$ – $\cdot 46$  mm. Segments 40–43. Colour brown (probably in part at least due to preservative). Prostomium short and rounded. Head-pore on dorsal surface of prostomium. No dorsal pores.

Setæ enchytræine in form ; there may, however, be a hint of a distal curve. In some bundles the inner setæ are smaller and slenderer than those at the ends of the bundle (*Fridericia* arrangement). In front of the clitellum the ventral bundles contain 4 or 5 setæ, occasionally 3 ; the lateral bundles have 3 or 4. Behind the clitellum the ventral bundles have 4 or 5, occasionally 3 or 6 setæ ; the lateral 4, 5, or 6, occasionally 3, or in the last segments even two.

The clitellum roughly covers segms. xii. and xiii. ; but in a specimen with fully developed sexual organs one-third of xi. was included, and a small portion of the hinder end of xiii. (about a quarter) was free.

A taste-organ is present on the floor of the pharynx, in front of the level of the dorsal pharyngeal mass and of furrow 2/3. It is best seen in longitudinal sections, according to which it is a solid transverse ridge, bent somewhat forwards, with a narrow free edge. Its base is slightly narrowed (antero-posteriorly, as seen in longitudinal sections), and its total height is about five times the antero-posterior thickness of its base of attachment. It is composed of elongated cells, and being solid is distinguishable from the other ridges of the ventral pharyngeal wall, which are merely folds of the epithelium. In one specimen the pharynx is being everted ; it is the ventral wall alone that comes forward here, and the taste-organ is at the tip of the everted part, so that it comes just onto a level with the mouth-opening, or in one or two sections rather further, projecting a little from the mouth. Some deeply staining matter is apparently being taken in.

The septal glands are bulky ; the last is in relation with septum 6/7, covering both sides of it and thus occupying part of segm. vii.

There are dorsal and ventral œsophageal nephridia. The dorsal organ ends behind in segm. vi., and gives a branch dorsalswards just in front of its ending ; in front it gets into segm. v. in one series of sections, and ends some distance above the œsophagus and not in contact with it. In another specimen, cut into longitudinal sections, it is confined to vi., and appears as a projecting mass dorsally on the œsophagus, spongy in texture, hardly staining, irregular in shape, and in intimate connection with the dorsal vessel ; indeed, a proper wall of the dorsal vessel is wanting, or cannot be distinguished, and the blood appears to be contained within a sinus in the nephridial tissue.

The ventral nephridium ends behind by branching into two at a level just in front of that of the end of the dorsal organ ; each branch extends laterally for some distance, and then terminates by turning somewhat forwards. These branches form the chief part of the organ ; the median portion, on the ventral œsophageal wall, is soon lost, and does not seem to get forwards into segm. v. This nephridium also is in close relation with blood-spaces—in this case those of the alimentary wall (text-fig. 1).

In another specimen both organs appear to be confined to segm. vi.

Besides these organs, which have, from their texture, more or less the appearance of nephridia, there is behind the pharynx a narrow diverticulum of the alimentary tube, wedge-shaped or conical as seen in longitudinal sections, pointed above, directed dorsalwards and backwards, and at its tip connected with a pair of solid knobs, the postpharyngeal bulbs. Each knob is a cellular mass, ovoid or somewhat club-shaped, with the long diameter continuing the direction of the diverticulum. The length of the diverticulum is  $120\ \mu$ , that of the bulbs  $36\ \mu$ , and the thickness of the latter  $20\ \mu$ .

Text-figure 1.



*Henlea (Henlea) brucei*; transverse section through oesophagus and hinder end of ventral oesophageal nephridium. *Bl.*, blood in sinus-like cavities of nephridium; *chl.*, chloragogen cells; *oes.*, oesophagus; *v.n.c.*, ventral nerve cord; *v.neph.*, ventral oesophageal nephridium.

The oesophagus is narrow as far as segm. viii., where it swells out into the intestine. The canal is thenceforwards swollen segmentally in an ovoid manner, and is not constricted in the genital segments. There are no chylus-cells.

Chloragogen cells begin, but only scantily, in the posterior part of segm. vi.

In segm. viii. is a pair of oesophageal diverticula. Each is sac-like, with folded walls; each originates from the alimentary tube at the hinder end of the segment, and extends forwards to its anterior limit. There appears to be some variation in the exact manner of origin of the sacs; in two series of sections, both longitudinal, the sacs have independent openings into the oesophagus,

one on each side; in a third, a transverse series, the two sacs join dorsally above the alimentary tube before they enter it.

The dorsal vessel originates in segm. viii. between the two cesophageal sacs. The blood was colourless (no red staining with eosin—absence of hæmoglobin).

The cœlomic corpuscles are few in number, large, disc-like, oval, about  $30\mu$  in long diameter; the body is granular, and a nucleus is present,  $3\mu$  in diameter, with a more deeply staining dot-like nucleolus. In one specimen the corpuscles were distinctly smaller than in the others—only  $20\mu$  long.

The preseptal portion of the nephridia is often pyramidal in shape, narrow at the free end and broader where it joins the septum; in any case it is of some length ( $40$ – $60\mu$ ). The postseptal portion is broad and ovoid or pear-shaped, with the wider portion behind. The duct is narrow, cylindrical, and long—as long as or longer than the postseptal portion; it is curved, arched, or even bent into a loop with the convexity backwards.

The testes are small, compact, either slightly lobed or not, but not divided (that is, not split up into a number of elongated pear-shaped divisions attached in a cluster at their narrow ends, as is the case in the genus *Lumbricillus*). A few sperm-morulae lie loose in segm. xi.

The funnels are small, with a distinct rim of nucleated cells, and resemble what is known as a “thistle-funnel.” Each is rather longer than broad; in different specimens they measured  $92$  by  $56\mu$ ,  $100$  by  $72\mu$ , and  $120$  by  $100\mu$ .

The first portion of the vas deferens, which lies in front of the septum, is  $16\mu$  in diameter; it very soon pierces the septum, and after maintaining its former size for a short distance, contracts to a very narrow tube,  $5$ – $8\mu$  in thickness, which lies in a close coil ventrally in the anterior part of segm. xii. just behind the septum and behind the position of the funnel.

The penial body is of the lumbricillid type, spherical, compact, of definite form, enclosed in a muscular capsule, about  $120\mu$  in diameter. In one specimen it appeared to be rather shorter in vertical diameter,  $120\mu$  high by  $160\mu$  long.

The ovaries are small, and consist of club-shaped lobes. Ova lie in segm. xii.

The spermathecal duct is cylindrical, about  $30\mu$  in diameter, with thick walls and small lumen; there are no gland-cells either on its course or round its ectal end. The ampulla is cylindrical or ovoid, thin-walled,  $40\mu$  in cross-section. There is a direct connection between the ampullae of the two sides across the middle line dorsal to the cesophagus—a fairly wide passage  $24\mu$  in diameter, with a lumen of  $16\mu$ ; this connection between the two ampullae is contiguous to the cesophageal wall, but there is no communication with the cavity of the cesophagus, a double layer of cells, the alimentary epithelium and the spermathecal epithelium, always intervening.

In another specimen, although the ampullae were more swollen



than in that from which the above description was taken and contained spermatozoa, I could not make out any connection between the two chambers: here again there was no communication between the cavity of the spermathecal apparatus and that of the œsophagus.

There are no copulatory glands.

The present species is not very unlike the common *H. nasuta*, which has been recorded from N. Russia and N. Siberia. It differs, however (I take as the standard of comparison Welch's description, 22), in being smaller, in having a blunt prostomium, in the shortness of the ventral œsophageal nephridium, in the male funnel being here more nearly spherical, in having no glands at the ectal end of the spermathecal duct, in having a broader communication between the two ampullæ, and in having no communication between spermathecæ and œsophageal lumen.

It also approaches *H. urbanensis* Welch, found in Illinois (19). The present species is smaller than that one, has fewer setæ in the ventral bundles, the ventral œsophageal nephridium is smaller, the dorsal vessel originates in viii., not in ix., the male funnel is much shorter, there are no gland-cells round the ectal end of the spermathecal apparatus, and no communication with the alimentary canal.

In many species of *Henlea* the inner ends of the two spermathecæ are bent downwards, meet, and join to form a common passage which enters the dorsal surface of the œsophagus. In both the species here described the condition is rather different; instead of meeting at an angle, the spermathecæ of the two sides are continued directly into each other across the middle line, and there is no communication with the œsophagus. This absence of communication is just possibly due to the specimens not being completely mature—the œsophageal connection being probably the last portion of the apparatus to form,—though from the condition of the other organs this hardly seems to be the case.

#### HENLEA (HENLEANELLA) sp.

Spitsbergen; among mosses on the bank of a fresh-water pond, more or less under water, Bruce City; from August 1st to 8th. Five specimens, none fully sexual.

Unfortunately the specimens are rather too immature to describe. They belong to that section of the genus which has no œsophageal sacs.

The dorsal and ventral œsophageal nephridia attracted my attention. The dorsal is seen in segm. vi. with a central lumen and lateral branches of some size; from this portion is continued back a solid cellular cord, regular in form, cylindrical and well defined in the middle line on the œsophagus as far as segm. x.; the cord, although it has no lumen, seems to take the place of the dorsal vessel, which is not separately visible. The ventral



œsophageal nephridium is confined to segm. vi.; it consists mainly of two masses, one on each side of the middle line; each mass has folded walls and a considerable lumen.

#### HENLEA (HEPATOGASTER) sp.

Spitsbergen; among mosses on the bank of a fresh-water pond, more or less under water, Bruce City; end of July and beginning of August 1921. A single specimen.

This specimen was taken near the last, but in a different moss-zone. The œsophageal diverticula take the form of a number of communicating tubules, as in the worms called *Hepatogaster* by Cejka (3) and in *Henlea tubulifera* and *H. moderata* as described by Welch (18, 19). I could not discover whether there were or were not dorsal and ventral œsophageal nephridia, as my sections of the worm were not very successful. The dorsal vessel begins in segm. ix.

#### Genus LUMBRICILLUS Örst.

##### LUMBRICILLUS ÆGIALITES, sp. n.\*

Spitsbergen; in seaweed at high-tide mark on shore, at head of Klaas Billen Bay in Icefjord, by Bruce City; last week in August 1921. Numerous specimens.

Length up to 17 mm.; maximum diameter .65 mm. Colour brownish (fixed in Bouin). Segms. 52-53. Prostomium rounded, hemispherical. Head-pore not made out with certainty, probably present.

A cuticle is not usually separately discernible; it is sometimes seen in the anterior segments, when it is not more than  $1\mu$  in thickness.

Fairly numerous deeply staining (with hæmatoxylin) mucous cells are seen in transverse rows in the surface epithelium—not, however, causing eminences on the surface.

Clitellum  $\frac{1}{2}$ xi.-xiii. ( $=2\frac{1}{2}$ ), not very well marked.

Setæ enchytræine (distal portion straight), blunt. In the ventral bundles in front of the clitellum 4 or 5 setæ; behind the clitellum 3, or at the hinder end 2. In the lateral bundles in front of the clitellum 3; behind, 3 in most segments, 2 at the hinder end.

The septal glands are in segms. iv., v., and vi.; septum 6/7 is bulged backwards by the last gland.

There are no salivary glands. There are, however, a pair of postpharyngeal bulbs—club-shaped structures in connection with the dorsal wall of the alimentary tube at the junction of pharynx and œsophagus. Their total length is  $240\mu$ ; they are constituted by a solid mass of cells in the form of a knob, and a stalk which

\* 'Αἰγιαλίτης, of the shore.

is attached to a small diverticulum of the alimentary tube; this might be expressed by saying that the proximal portion of the stalk is hollow, its cavity communicating with the alimentary lumen.

In the œsophagus are large numbers of parasitic Ciliata. The œsophageal epithelium is being shed *en masse* into the lumen of the canal; in some places also the cilia are being detached and shed.

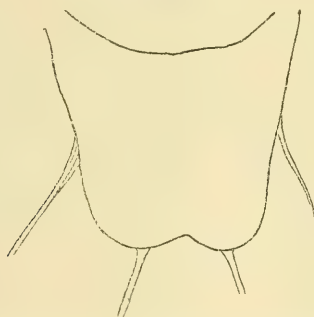
The intestine dilates gradually after passing through the genital segments, about segm. xiii.

Chloragogen cells begin in segm. vi.

The coelomic corpuscles have a length of  $16-24\mu$ ; in shape they are elongated, fusiform, pear-shaped, or oval. They are not very definite structures, and often seem to be disintegrating and of irregular outline. Some, broader than most, are nucleated.

The dorsal vessel begins in segm. xiv. The blood from its staining reactions (it stains a pinkish-brown with eosin) probably contained hæmoglobin.

Text-figure 2.



Cerebral ganglion of *Lumbricillus agialites*.

The anteseptal portion of the nephridia consists of the funnel only. The postseptal portion is spindle-shaped. The stout duct is the hinder end of the organ bent downwards and inwards, sometimes forwards as well; sections of the duct are rather characteristic—always oval in outline and showing radial striations in the wall.

The cerebral ganglion (text-fig. 2) has a slightly concave anterior border; the posterior border is slightly indented in the middle line and rounded on each side of the median indentation. The ganglion is about as long as broad, and is broader in front than behind.

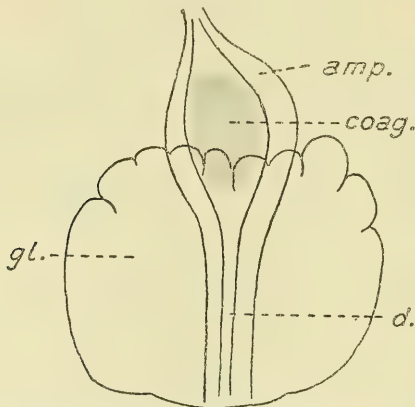
The testes have the usual constitution in the genus. Each consists of a number of elongated lobes ("divided" testes, using Welch's term), which extend into segms. x. and xi.; each lobe is contained in a membranous sac, which in some cases may be fairly

substantial, with a number of much elongated nuclei in its wall. The substance of the lobes consists proximally of a mass of cells only; further from their attachment they dissolve into sperm-morulae, still contained within the sacs. There is a large vacancy in septum 10/11; as already said, the lobes of the testes extend into both segments.

The funnel is short and stout—about twice, or at any rate not more than three times, as long as wide. In a specimen in which the funnels were isolated by dilaceration they were not more than  $1\frac{1}{2}$  times as long as wide. The vas deferens is long and much coiled, but in the dilacerated specimen not so tightly as in the next species; it is confined to segm. xii.; in diameter it measures 10–12  $\mu$ .

The penial body is compact, subspherical in shape, in diameter 130–160  $\mu$ , of the usual lumbricilline type, with a strong muscular capsule. It causes a slight projection on the surface.

Text-figure 3.



Spermatheca of *Lumbricillus ægialites* isolated by dilaceration. *Amp.*, ampulla; *coag.*, coagulum in ampulla; *d.*, duct; *gl.*, mass of gland-cells.

The ovaries are in segm. xii.; loose ova are present in xii. and also in xiii. There is no ovisac. The female funnels are merely backward bulgings of the septum. The oviducts are not as yet patent.

The spermathecal ampulla is smoothly ovoid, 90–100  $\mu$  in diameter, and communicates with the œsophagus by a rather narrow neck. The duct is straight and as long as the ampulla. A large mass of gland-cells surrounds the duct, and takes up all the space between the parietes and the ampulla—even surrounding the basal half of the ampulla; the upper margin of this mass of gland-cells is slightly lobed (text-fig. 3).

Copulatory glands ("ventral glands") are present in segments

xiv. and xv. They are small, and the wings do not meet above the cord, all the dorsal surface of the cord being free. The lateral extent of the wings is not great; each measures about twice the transverse diameter of the cord, and does not reach outwards more than halfway towards the ventral setal bundles. They are not composed of several layers (as in *L. nervosus*, according to Ude).

Besides the parasites in the œsophagus, others were found in the testicular region. Here there are a number of sacs, each containing what appear to be stages in the formation of spores.

It is extremely difficult to know which of the worms described by the older writers, and designated by names that are still in use, correspond to forms met with at the present day. The older descriptions are so very scanty, according to present-day requirements, that they frequently fit several of the species now recognized. In course of time, other descriptions have been published under the older name, supposedly referring to the same worm; particulars have been taken from these descriptions and incorporated in the diagnoses. The result is a composite picture, which may or may not represent the worm which the original describer had under his eyes. Another worm may come up, which may fit the original description equally well—and may therefore be identical with the original species; but it will have to be described as new, since it is not characterized by the accretions which have gathered round the original diagnosis.

Thus the original description of *Lumbricillus pagenstecheri* (Ratzel) is very scanty, but it has been added to by Vejdovsky and Ude. The present worm seems to differ from the original description (12) in having the setæ fewer in number (2-5 as against 6-10, 7-8 being the commonest numbers in the original), and straight (those of the original, while described as straight, had, nevertheless, a slight curve at their sharp end—"mit leichter Biegung an der scharfen Spitze"), with blunt instead of sharp points. From the diagnosis in the 'Tierreich' (11), which embodies what I have called later accretions, it differs in having small instead of large copulatory glands, which leave the whole of the dorsal surface of the cord uncovered; and in having the whole of the spermathecal duct closely covered with gland-cells, instead of loosely; the shape of the cerebral ganglion also differs considerably.

From *L. henkingi*, described by Ude from Bear Island, the present form differs in not having S-shaped setæ, in the origin of the dorsal vessel in xiv. (instead of in xiii.), in having copulatory glands in xiv. and xv. (instead of in xiii. and xiv.), and in the fact that these glands are here very much smaller (in *L. henkingi* the wings of the glands are four times as extensive as the greatest diameter of the cord, and they reach outwards somewhat beyond the setal bundles).

The present species is not very unlike *L. franciscanus* Eisen, from California (varieties of the species also from Pribilof Islands

and Alaska). It differs apparently in the shape of the setæ, in the place of origin of the dorsal vessel (in *L. franciscanus* it arises, according to the short diagnosis, in segm. xiv. or xv., but in the detailed description it "has already arisen in xvi. How much further posteriorly it extends I do not know, as I did not section further"), in the rather greater extent of the clitellum, and in the more restricted distribution of the copulatory glands (clitellum over segms. xii. xiii., glands in xiv.-xvi. in *L. franciscanus*).

*LUMBRICILLUS NECROPHAGUS*, sp. n.\*

Spitsbergen; in dead seal, at high-tide mark on shore, by Bruce City at head of Klaas Billen Bay in Icefjord; 25.vii.1921. A number of specimens.

Length up to 15 mm.; maximum diameter .4-.55 mm., but many are thinner. Colour pale yellowish. Segments 51-53. Prostomium blunt, rounded. No mucous cells in epidermis.

The surface is covered with a moderately thick cuticle, considerably thicker and more noticeable than that of the last species.

Clitellum  $\frac{1}{2}$ xi.-xiii. (=2 $\frac{1}{2}$ ); in sections the extent appears to be rather different—it includes a little of xi. and gets slightly on to xiv. also.

The setæ are enchytræine in form (I think I have occasionally detected a hint of a distal curvature) and blunt, rounded, or even squarish at their tips. The ventral bundles contain in front of the clitellum mostly 4 (occasionally 5 or 3) setæ and behind the clitellum 3. The lateral bundles have usually 3 (occasionally 4 or 2) in front of, and 3 or 2 behind, the clitellum.

The septal glands are bulky, the last, in segm. vi., causing a backward bulging of the septum.

The postpharyngeal bulbs arise from a transversely placed groove-like evagination of the alimentary tube behind the pharyngeal mass. Each is a slender elongated cord of cells, rather swollen at its distal end, its general direction nearly vertical, and solid except in its proximal third or less, where there is a narrow lumen.

Chloragogen cells begin in segm. v.

The œsophageal epithelium is being thrown off into the cavity of the tube; the cells lie loose in the lumen, and there is a copious granular substance between them and the remainder of the œsophageal wall. Similarly, the intestinal epithelium is disintegrating or has disappeared over large areas; the intestinal tube is full of a faintly staining granular substance, or of what is apparently a disintegrating cell-mass; sometimes the epithelium is separating in sheets, and the lumen is half empty. The intestinal tube is much swollen out, and the cœlom is almost obliterated in parts, the nephridia being pressed against the

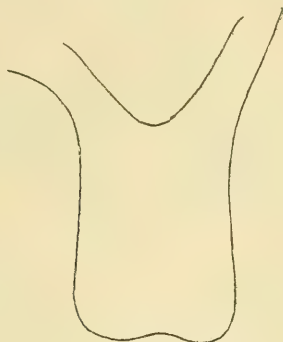
\* *Νεκροφάγος*, devouring corpses.



body-wall. Extreme degeneration may exist throughout the whole of the alimentary tract behind the septal glands.

This condition might be due to the presence of parasites—there are a number of such, elongated, cylindrical, with a nucleus of corresponding shape, in the œsophagus (probably Ciliates, though no cilia could be made out on them), as well as a number of small cysts in the tissues. Still, the usual Ciliate parasites of the œsophagus of Enchytræids do not as a rule cause such degeneration. It might perhaps be due to the parasites of the tissues, through their metabolic products, which may have a specific action on the alimentary epithelium. Or one might attribute it to the food (assuming that the worms were taking in material from the body of the dead seal in which they were found), but for the fact that the last species also showed degeneration of the alimentary epithelium, though not to such an extreme degree as these worms.

Text-figure 4.



Cerebral ganglion of *Lumbricillus necrophagus*.

A lightly staining, almost perfectly homogeneous, very slightly granular coagulum, containing many nuclei, almost fills up the coelom in the anterior part of the body. There are no definite lymph-corpuscles of the type of those found in the former species; but the nuclei in the coagulum just described seem to have belonged to corpuscles which have degenerated. These changes seem to go along with those in the intestine, and are doubtless due to the same cause.

The dorsal vessel begins in segm. xiv. The blood contained hæmoglobin.

The anteseptal part of the nephridia is quite small and shortly cylindrical. The postseptal portion is elongated and is continued behind into the duct, which has the same structure as in the last species. The whole is flattened against the body-wall.

The cerebral ganglion is rectangular in general outline (text-fig. 4), the sides being approximately parallel and the length

about one-third greater than the breadth. The posterior border is very slightly indented, and the posterior angles are well rounded.

The testis consists of numerous lobes or divisions, each contained in a definite sac; in each sac the distal portion of the contents consists of morulae and developing spermatozoa. The lobes are contained in segms. x. and xi.; they originate from the parietes on both sides of the attachment of the septum. Numbers of spermatozoa are free in segm. xii. at and behind the level of the penial bodies and as far back as the hinder end of the segment. Numerous cysts containing developmental stages of parasites occur amongst the testis-lobes.

In two specimens from which the male deferent apparatus was isolated by the method of dilaceration, the funnels appeared to be only a little longer than broad—not more than half as long again as broad. In one specimen, in which they were well seen, they were rather triangular in shape, the posterior end (where the vas

Text-figure 5.



Spermathecae and intervening part of oesophagus of *Lubricillus necrophagus*, isolated by dilaceration. *Amp.*, ampulla; *coag.*, coagulum in ampulla; *d.*, duct; *gl.*, mass of gland-cells; *oes.*, oesophagus.

deferens is given off) being narrow. In sections also the funnels appeared short and stumpy, the proportions varying, but apparently most often about half as long again as broad.

The vas deferens is narrow,  $8\ \mu$ , and is confined to segm. xii.; it is tightly coiled, and is seen in sections as a number of windings squeezed close against the body-wall. The penial body is of the lumbricillid type, ovoid, somewhat flattened vertically, .19 mm. long and .14 mm. high.

The large ovary, in segm. xii., is also branched into lobes.

The spermathecal ampulla is shortly and stoutly pear-shaped, drawn out above into its oesophageal connection; there appears to be a communication between the cavities of the spermatheca and of the oesophagus. The duct is well marked off, longer than the ampulla, and surrounded by a large lobed mass of gland-cells which fills up the space between the parietes and the base of the ampulla (text-fig. 5).

Copulatory glands occur in segms. xiv. and xv. They are small,

not covering the dorsal surface of the cord; their shape is slightly different from those of the last species; the lateral expansions are level with the dorsal surface of the cord, so that there is a straight line all along; in the former species the wings rise above the level of the cord.

I was at first extremely inclined to unite these worms with the last species; and I am still not quite certain that they are specifically distinct. The chief difference is that there are no mucous cells in the present specimens; they were stained in exactly the same way as the former, yet the mucous cells are extremely obvious at the first glance in the former preparations, while they are entirely absent in these. The thicker cuticle also seems to be a distinction, as well as the shape of the cerebral ganglion and, possibly, though doubtfully, the different shape of the copulatory glands. The appearance of the two worms is also very different; *L. ægialites* is dark brown (perhaps in part due to the fixative—Bouin), *L. necrophagus* pale and semi-transparent (fixative not stated); *L. ægialites* appears much stouter than *L. necrophagus*, though actual measurements hardly bear this out. But the two are closely related; whether the differences can be put down to the different manner of life in the two cases seems doubtful, since one can hardly suppose that the occurrence of these specimens in a dead seal was more than accidental.

#### Genus ENCHYTRÆUS Henle em. Mich.

##### ENCHYTRÆUS ALBIDUS Henle.

Bear Island; Walrus Bay (S.E. of island); by shaking plants of dry tundra; 15.vi.1921. Four specimens, some of them (? all) mature.

Same locality; among plants on shaly slope; 22.vi.1921. Two specimens, both mature.

Same locality; among plants on top of hill (dry tundra); 22.vi.1921. Two specimens, both mature.

##### ENCHYTRÆUS CRYMODES, sp. n.\*

Spitsbergen; among mosses on the bank of a fresh-water pond, more or less under water, Bruce City; end of July and beginning of August 1921. Several specimens.

Spitsbergen; moss by salt marsh, probably reached by extremely high tides, near Bruce City; 8.viii.1921. Numerous specimens.

Mr. Elton adds a note to the above data:—"These" (the second of the two batches) "were observed to be living on live moss leaves, and seemed to occur among these, but not in the decaying parts of the moss. They survived being frozen solid, in an experiment which I did."

\* Κρυμώδης, icy cold, frozen.

Length 8-9 mm.; diameter .4 mm. Colour brownish. Segments 34-38. Prostomium bluntly triangular, the triangle being about equilateral. Head-pore between prostomium and first segment; no dorsal pores.

Clitellum not well marked (or scarcely formed), xii.-xiii. (=2).

Setæ enchytræine in form, tip fairly sharp. In front of the clitellum both ventral and lateral bundles have three setæ, occasionally four; behind the clitellum they have two only.

The hindmost septal glands are in segm. vi.

There are no salivary glands of the type of those of *E. albidus*, but, as in the species of *Lumbricillus*, there are a pair of post-pharyngeal bulbs. These are small, knob-like, ovoid cell-masses immediately behind the pharynx, connected with the first part of the œsophageal tube by solid conical cell-aggregates. The knobs are separated from each other in the middle line by a muscular strand. In other preparations of these same worms the structures are not so clearly seen—either there is actually some variation or the plane of section is not so favourable.

Chloragogen cells begin scantily in segm. v.

The œsophagus remains narrow till past the genital segments; it begins to widen in xiii. and the intestine is fully established in xiv. There are numerous sporozoan parasites in the epithelium of the œsophagus. There are no chylus-cells in the alimentary tract.

The dorsal vessel originates in segm. xiii. The blood stains slightly with eosin; probably there was a small amount of hæmoglobin in it originally.

Cœlomic corpuscles are present as irregular discs, staining little, fusiform or oval in shape,  $32\mu$  in average length (the limits being  $30-40\mu$ ), nucleated; but they are relatively few in number.

The nephridia (text-fig. 6) have a small narrow anteseptal portion; the postseptal portion is swollen out, shortly ovoid or subspherical. The duct is long, relatively thick, and leaves the outer side of the postseptal mass, passing backwards for some distance and then downwards—even somewhat forwards in some sections.

The testes are bulky in the present specimens; they are slightly lobed in their distal portions. Some of the sexual cells are becoming metamorphosed into sperm-morulæ and spermatozoa, and these are bound together and to one of the lobes of the testis by an apparently incomplete sac. These sacs appear to be rupturing, and so allowing their contents to escape. In one specimen there is a mass of genital cells in segm. ix.

The funnels are long and narrow, as much as 6-8 times as long as broad. They may push right through the septum into segm. x., in which the anterior half of the funnel may thus be contained; or the anterior end may be reversed and push back septum 11/12 so as to form a sac, in which the anterior part of the funnel is contained. The mouth of the funnel has a distinct lip.

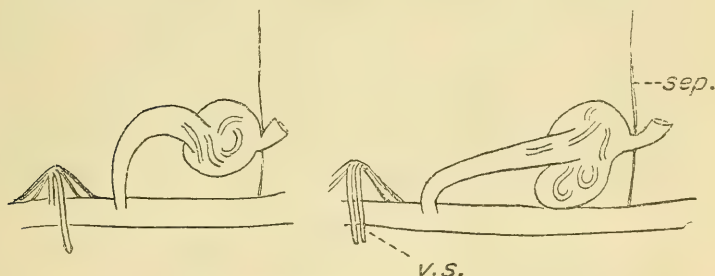
The vas deferens is narrow, 7–12  $\mu$  in diameter, and forms numerous close coils in segm. xii., to which it is confined. It pierces and penetrates the penial body.

The penial body is of moderate size, .12 mm. in diameter, compact, of the lumbricilline type, spherical, with a definite muscular capsule.

The ovary, in segm. xii., is bulky. Septum 12/13 is bulged back by ova contained in segm. xii. in such a way as to form an incipient ovisac.

The spermathecae have each a relatively small and thin-walled ampulla, subspherical in form, 80–120  $\mu$  in diameter. The duct is thick-walled with high epithelium, 70–80  $\mu$  in diameter, cylindrical, longer than the ampulla and nearly as thick. There are a number of pyriform groups of cells round the ectal end of the duct. The ampulla, probably communicates with the cavity of the oesophagus at full sexual maturity, though such a patent communication was not visible in my specimens; in one, however,

Text-figure 6.



Nephridia of *Enchytræus crymodes*.

Sep., septum; v.s., ventral setal bundle.

the epithelium of the two organs (ampulla and oesophagus) was continuous. The two ampullae may be separated from one another by a part of the oesophagus; but in another case they were contiguous—indeed, their walls were fused together. In both these cases the cavity of the ampullae contained spermatozoa.

Copulatory glands are present, though small, in segms. xiii. to xvi. and perhaps xvii. They do not cover the dorsal surface of the cord at all. There is a small rounded papilla over the position of each gland where the gland-cells come to the surface.

#### ENCHYTRÆUS sp.

Spitsbergen; among moss in marshy (fresh-water) area near Bruce City; 8. viii. 1921. A number of specimens.

I regret that this worm is rather too immature to justify my giving it a name. I append a few particulars, which may enable it to be identified when next it is met with.



Length 3-3.5 mm.; diameter .17 mm. Segments 22, or 22 with some incomplete segments behind. Colour dark. Setæ enchytræine in form, two per bundle throughout the body. No salivary glands. Cœlomic corpuscles fairly numerous, oval, nucleated, 12-14  $\mu$  in length. The dorsal vessel originates in segm. xii. The nephridia have a large anteseptal portion, nearly as large as the postseptal; the duct undergoes several windings in the anteseptal portion; the organ is somewhat constricted at the septum; and the postseptal portion is elongated, the duct being continued from the hinder end.

The testes were in an early stage, of large size, taking up a very large part of segm. xi.; scarcely any sperm-morulæ had formed, the testes were lobed, but not "divided." The funnels were very small, and twice as long as broad; but it is more than likely that these proportions would not be maintained throughout the further development of the organ. There was a small, ovoid, and well-defined penial body.

The ovaries were lobed in the same manner as the testes. The spermathecal ampulla was short, subspherical, and the duct cylindrical, entirely destitute of surrounding gland-cells. There were no copulatory glands.

The numbers of the setæ (2 per bundle throughout the body), the large anteseptal part of the nephridia, and the presence of a lumbricilline penial bulb constitute a group of characters which, along with the small size of the worms, may permit of recognition in the future; but I disapprove of the practice of giving names to incompletely described or immature material.

#### Genus MESENCHYTRÆUS Eisen.

##### MESENCHYTRÆUS sp.

Spitsbergen; among plants of dry tundra, Cape Boheman in Icefjord in W. Spitsbergen; 12.vii.1921. A single specimen.

Spitsbergen; among mosses on the bank of a fresh-water pond, more or less under water, Bruce City; end of July and beginning of August 1921. Two specimens.

Like the last, the present specimens are too immature to name.

Length 7-10 mm.; maximum diameter .6-.8 mm. Segms. 46-54. Colour dark brown. The worms are solid-looking, like the young of earthworms. A large head-pore near the tip of the proboscis. Setæ lumbricine in shape, stout and relatively short, with sigmoid curve; in the ventral bundles 4, 5, or 6 throughout the body; in the lateral 2 or 3 throughout, or sometimes behind the clitellum 4 or 5, and occasionally, in front of the clitellum, one only.

Cœlomic corpuscles rather small, 12-20  $\mu$ , granular, with deeply staining granules or network, and a small nucleus visible only with difficulty. No salivary glands; postpharyngeal bulbs

present. Œsophagus dilates fairly suddenly in segm. vii. Very numerous parasitic Ciliates in Œsophagus; parasites also in Œsophageal wall; a cyst outside, in the cœlom. Much of the alimentary epithelium is degenerating or has been shed. Dorsal vessel originates in xiv.; the blood stains with eosin. Nephridia of the type found in the genus; the duct goes backwards at first, then forwards, ending finally a very little way behind the inter-segmental groove, indeed almost in it.

Clitellum only slightly marked, extending over xii. and xiii. with the greater part of xi. also. Testes lobed, but not "divided." Sperm-sac present, extending into xiii. Funnel as yet merely a plate of cells on the septum; vas deferens only as a solid cord of cells, cylindrical and somewhat wavy, from funnel to male aperture. Penial bulb as a number of loosely arranged cells around the terminal portion of the vas deferens. Ovisac extending back to xvii. Spermathecal ampulla not distinguishable; duct narrow, no gland-cells round its ending, cylindrical, of some length, coming to the surface in the tract of the lateral line cells.

The distinction of species of *Mesenchytræus* depends largely on the characters of the vas deferens and spermathecal ampulla—just those portions of the sexual apparatus which are most undeveloped in the present specimens.

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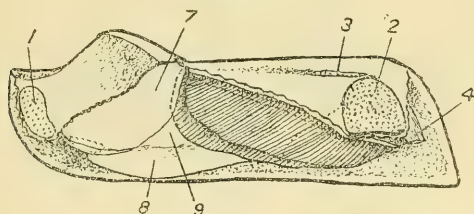
50. On the Anatomy of *Scaphula*, Benson, with a description of a new Species. By EKENDRANATH GHOSH, M.Sc., M.D., F.Z.S., F.R.M.S., Professor of Biology, Medical College, Calcutta.

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(Text-figures 1-7.)

The Lamellibranch genus *Scaphula*, Benson is represented by three species from the rivers of India and Burma. The anatomy of all the known species is unknown to science, with the exception of the gills of an undetermined species from Siam (Ridewood, Philosophical Transactions, Ser. B, vol. 195). The present paper aims at describing the characteristic soft parts of the genus, based upon the animals of *S. celox*, Benson, and of a new species from Siam. The specimens were received from the Zoological Survey of India, through the kindness of Dr. N. Annandale.

Text-figure 1.



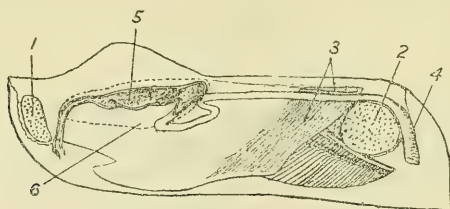
Animal of *S. celox*, side view (left).  $\times 10$ .

The body is elongated, being two to three times as long as it is deep, and deeper posteriorly than anteriorly. The median dorsal margin is a third to a quarter less than the body-length. The anterior adductor muscle is much smaller than the posterior. Both the anterior and posterior margins slope backwards. The anterior adductor muscle is narrow and elongated at its insertion, and is placed rather close to the anterior margin. The length of the area of insertion is parallel to the latter. The posterior adductor muscle is large at its insertion and may be oval or triangular in shape. It is placed a little distance from the posterior margin. The foot is elongated and compressed laterally; it presents a shallow fissure along the mid-ventral line. The foot is perhaps capable of slight expansion round the fissure. A minute byssus cavity is present in the ventral fissure towards the posterior end of the foot. The byssus is not well developed, being in the form of fine silky threads in the Siamese species. An obtusely-pointed process is present at the postero-ventral aspect

of the foot. The anterior retractor pedis muscle is narrow and elongated, and consists of two heads of insertion into the valve. The posterior retractor pedis muscle is narrow, and elongated at its insertion into the valves just in front of the posterior adductor muscle. It extends diagonally from the posterior end of the foot.

The visceral mass is greatly widened out laterally into a somewhat conical hump with an oblique ridge on the surface. The gills are elongated, tapering posteriorly, and are about half the length of the body and thrice as long as broad. The gill-axis is slender, rod-like, and is placed more horizontally than diagonally and ends in a small free posterior portion. The gill-filaments are placed obliquely to the gill-axis, and the reflected filaments are free dorsally. The labial palps are elongated, semilunar in shape, and are placed at an obtuse angle with the gill-axis. They are one-third to one-fourth the length of the body, and twice as long as broad. The œsophagus is curved, with the concavity directed backwards. The stomach is greatly elongated. The cæcum of

Text-figure 2.

Animal of *S. celox*, longitudinal section.

the crystalline style is small, narrow, and is fused with the beginning of the intestine, the latter being placed on the right side of the cæcum. The intestine consists of a short anterior and a long posterior limb, and is placed towards the right side of the body. The rectum is placed dorsally to the heart, and ends in a small free portion projecting downwards and backwards from the posterior surface of the posterior adductor muscle. The pericardium is divided into two lateral portions. The two ventricles are widely separated from each other by a narrow tube, which gives rise to anterior and posterior aortæ. The auricles are comparatively large; they do not communicate with each other. The digestive glands are extensive. The genital organs surround the lower portion of the œsophagus and occupy the ventral region of the visceral mass. Osphradia and Thiele's abdominal sense-organs are both absent.

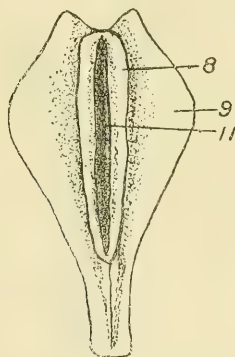
*Structure of the Gills of S. celox.*—The gill-filaments are flattened antero-posteriorly as usual. There are no interlamellar extensions (described in *Arca pexata* by Kellogg (Bull. U.S. Fish



Comm. 10, 1890) and in *Arca americana* by Ridewood, *l. c.* p. 199), but interlamellar septa (present in both the above species) are present, extending to about one-fourth or one-fifth the height of the filament. The ciliary discs seem to be present only at the free ends and at the junctions of the direct and reflected filaments. They are much more numerous in all the other known genera and species of the Arcidæ, being arranged in many horizontal rows. The arrangement of the cilia could not be followed distinctly. The frontal cilia do not seem to extend much on the anterior and posterior faces of the filaments. The lateral ciliary rows are placed a little distance behind the frontal row. The chitinous lining is uniformly thin.

The gills of the species of *Scaphula* from Siam could not be studied. Ridewood notes in species from Siam (the present species?) one horizontal row of ciliary disc to the descending filament and one to three such rows in the ascending one.

Text-figure 3.



Ventral view of the foot and visceral mass of *S. celox*.

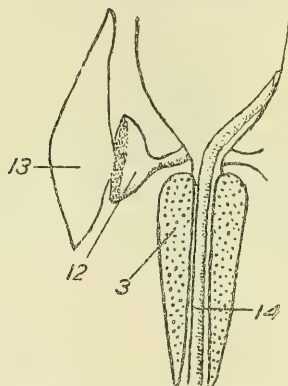
*Remarks.*—The genus *Scaphula* Benson belongs to the family Arcidæ. It was recognized as such by Gray (*Ann. & Mag. Nat. Hist.* xix.), and by Adams and Adams (*Gen. Recent Moll.*). Fischer (*Man. Conch.*) makes it a subgenus of *Arca*, and places it in the middle of his list. Dall (*Trans. Wagner Free Institute of Science*, iii, pt. 4) makes it a group in the subgenus *Barbatia*. Pelseneer (*Lankester's Treatise on Zoology*, v.) raises it to a genus, and places it near the genus *Arca*. Lamy (*Journ. Conchyliol.* lv.), in his revision of the genus *Arca*, considers it a subgenus, and places it near the subgenera *Arca*, *Barbatia*, *Acar*, *Fossularca*, and *Parallelepipedum*.

The body of the animal is characterized by an antero-posterior elongation, perhaps correlated with the inequality in the size of the adductor muscles. The elongation of the body has also affected the visceral mass and the foot to a relatively less extent. But

the shape, size, and the position of the anterior adductor muscle may have something to do with the atrophy\* of the extreme anterior region of the body. The poor development of the byssus apparatus and the absence of sense-organs are probably examples of degeneration due to its fluviatile life.

The animal of *Scaphula* agrees more with the animals of *Byssarca* Swainson, *Barbatia* Gray, and *Acar* Gray than those of the other genera of the Arcidae in its great antero-posterior elongation and in the inequality in size of the adductor muscles. It further resembles the first two, especially in the widening of the body from side to side, and in the great disparity of the adductor muscles in size. But the foot and the visceral mass are strongly affected in the present genus by the elongation of the middle region of the body, whereas in *Byssarca* and *Barbatia* these organs are comparatively less elongated, the elongation

Text-figure 4.



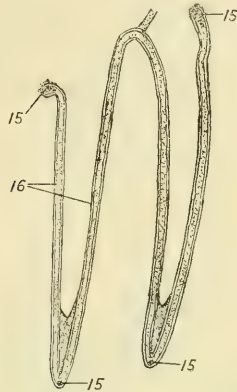
Heart (from the dorsal aspect) of *S. celox*.

being mainly exhibited in the posterior retractor pedis muscles. In *Acar* the body seems to be equally elongated in the middle region (the above-mentioned parts being affected) and in the posterior region beyond the posterior adductor, the mantle only being affected. The elongation of the posterior region of the body is thus greatest in *Acar*, least in *Byssarca*, and attains an intermediate condition in *Scaphula*. With regard to the heart of *Scaphula*, we find an intermediate condition of the ventricles between *Byssarca* (with a wide separation of the ventricles) and *Barbatia* (in which they are only slightly separated), but marked difference from *Acar*, which has a single, but distinctly, bilobed ventricle. The position of the heart in relation to the rectum might have been derived from a condition seen in the above genera. Lastly, the projecting portion of the rectum seems

\* This is not referred to elsewhere.—ED.

to bring the anus directly in the line of the outward current of water and the exhalant aperture, and this is perhaps correlated with the depth of the posterior region below and behind the posterior adductor. In *Acar* the great depth of the mantle is attended by a great elongation of the projecting tube of the

Text-figure 5.

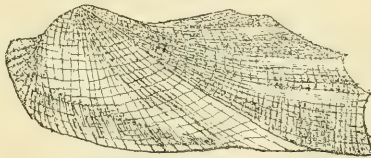
A gill-filament of *S. celox* (outer and inner demibranch).

rectum. In conclusion it might be noted that the present genus might have originated amongst and be related to *Byssarca* and *Barbatia*, although modified and perhaps degenerate owing to its fluviatile life.

#### SCAPHULA MINUTA, sp. n.

Specimens of this species were collected by Dr. N. Annandale, who kindly gave me the following information:—The species occurs all over the Tale Sap or Inland Sea of Singgora on the

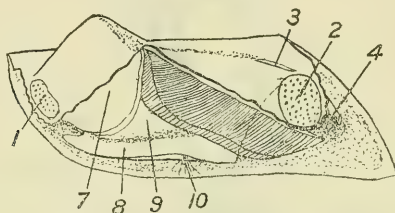
Text-figure 6.

Shell of *S. minuta*, outer surface (left valve).

east coast of peninsular Siam. It was found attached to weeds and stones in both fresh and brackish water. The specimens I have examined were found adhering to water-plants by several byssus threads.

*Shell*.—Minute, elongated, thin, closed and deep posteriorly. Anterior margin slightly convex, and sloping backwards from above and continuous with the ventral margin. Ventral margin slightly convex in front, straight or very slightly convex behind and somewhat sloping downwards. Posterior margin convex and sloping downwards and backwards. Ligamentous area small, narrow, triangular in front of and broadly club-shaped behind the umbones. Ligament lozenge-shaped and occupying the anterior and a small area of the posterior portion of the ligamentous area, and half the length of the entire ligamentous area. Hinge teeth numerous. Central teeth obsolete. Four or five lateral teeth, oblique in direction. Three posterior lateral teeth elongated and very oblique. Surface with a thin, light-brown epidermis. Diagonal ridge very prominent. Surface in

Text-figure 7.

Animal of *S. minuta*, side view (left).

front of the ridge convex, and with fine radiating and horizontal lines intersecting one another. Surface behind the ridge concave, and with four stout radiating ridges in addition to minute, closely placed similar lines all intersected by vertical ones. Length 4.5 mm., height 2 mm., trans. diam. 2 mm.

The present species differs from the three other known species of *Scaphula*, Benson in its minute size, in the slight tumidity of the valves (the proportion of the vertical diameter to the transverse diameter being 1:2), and in the comparative shortening of the body in the antero-posterior diameter.

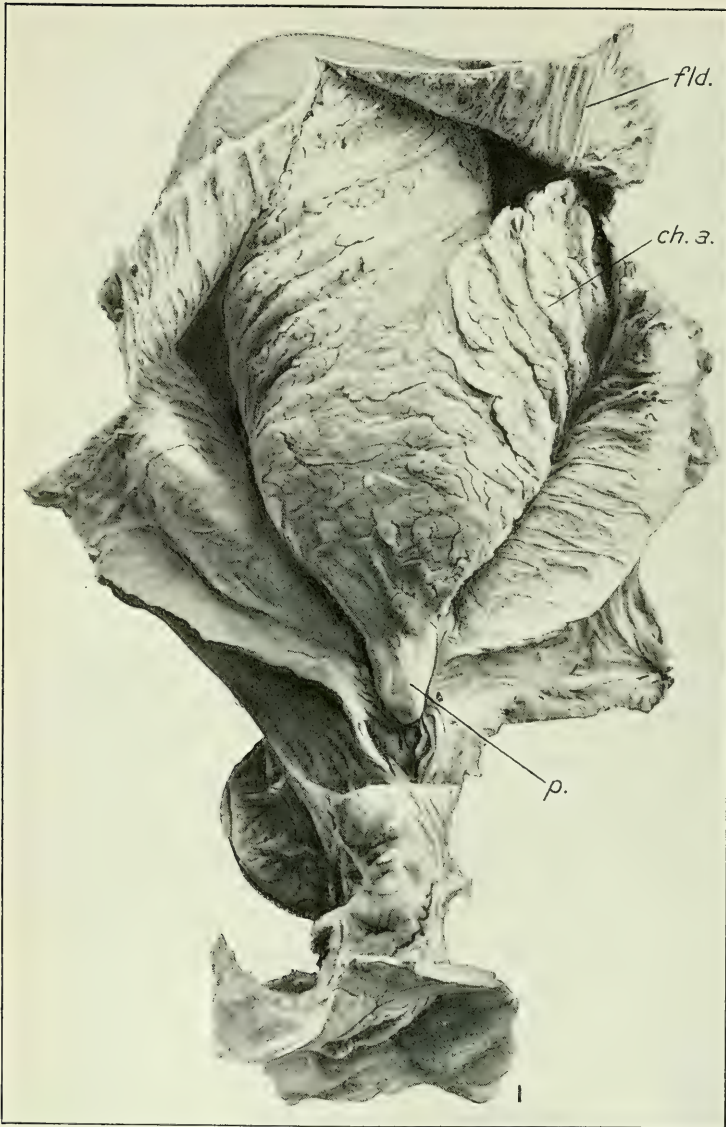
The type-specimens are kept in the Indian Museum.

#### *Explanation of Text-figures 1-7.*

1. Anterior adductor muscle. 2. Posterior adductor muscle. 3. Posterior retractor pedis muscle. 4. Free end of the rectum. 5. Stomach. 6. Outline of the liver. 7. Labial palp. 8. Foot. 9. Visceral mass. 10. Byssus threads. 11. Ventral fissure of the foot. 12. Ventricle. 13. Auricle. 14. Rectum. 15. Ciliary discs. 16. Filament of inner demibranch.

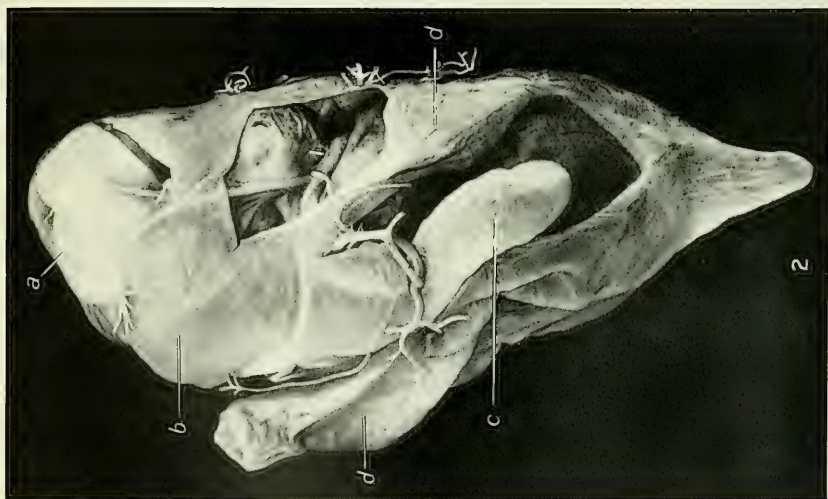
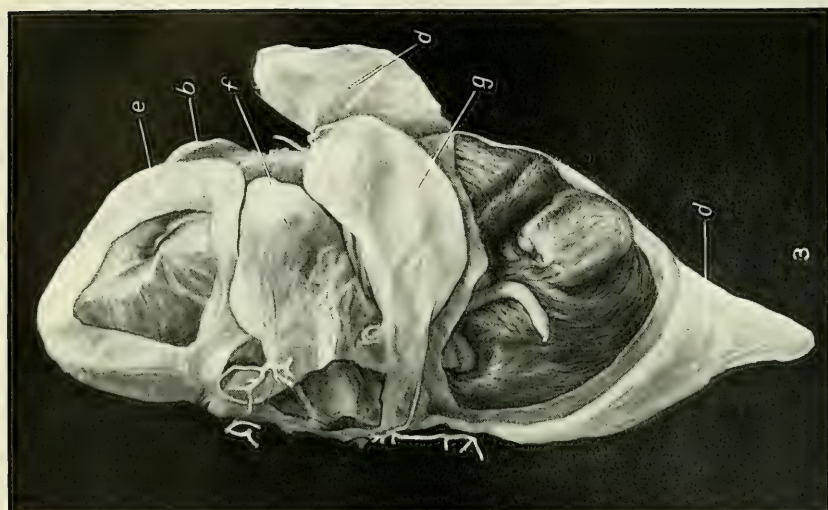






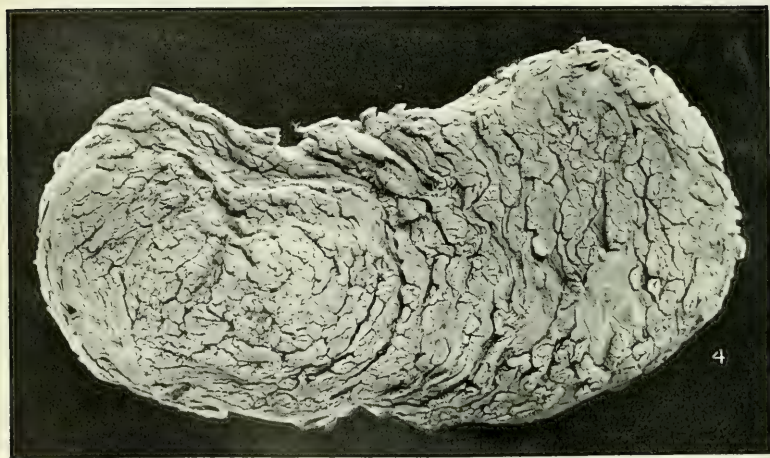
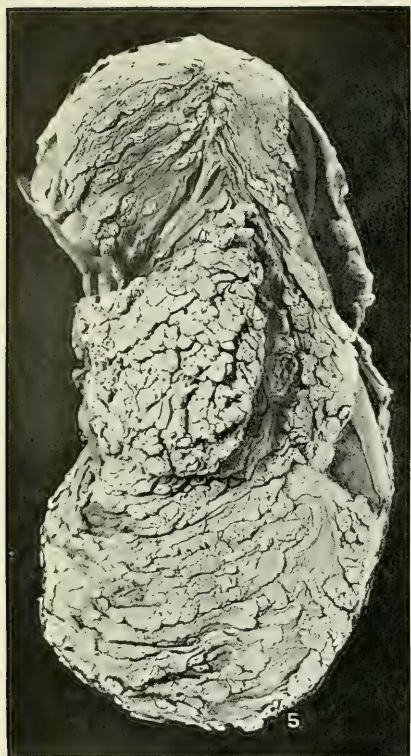
FŒTAL MEMBRANES OF *CHIROMYS MADAGASCARIENSIS*.





FŒTAL MEMBRANES OF *CHIROMYS MADAGASCARIENSIS*.





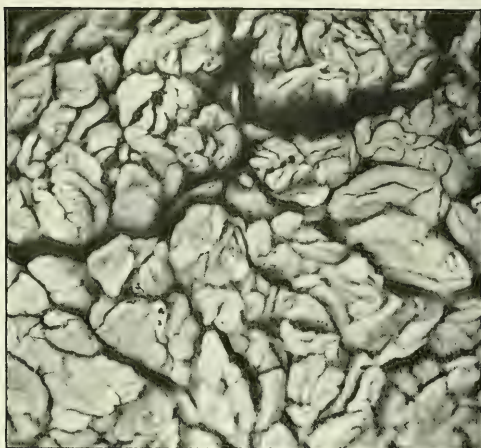
FÆTAL MEMBRANES OF *CHIROMYS MADAGASCARIENSIS*.





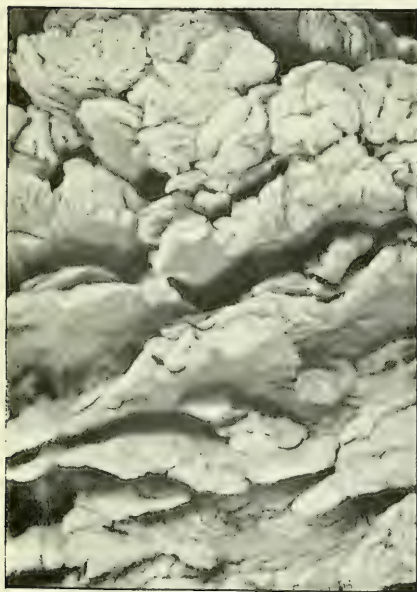


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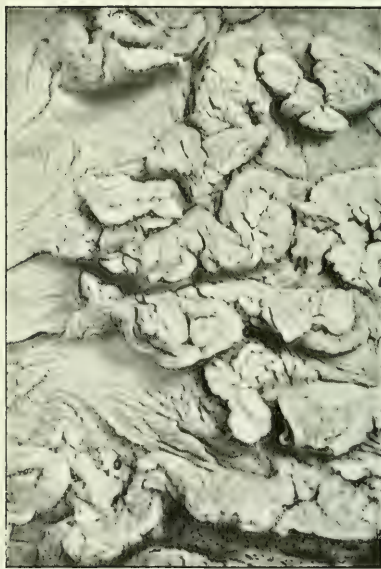


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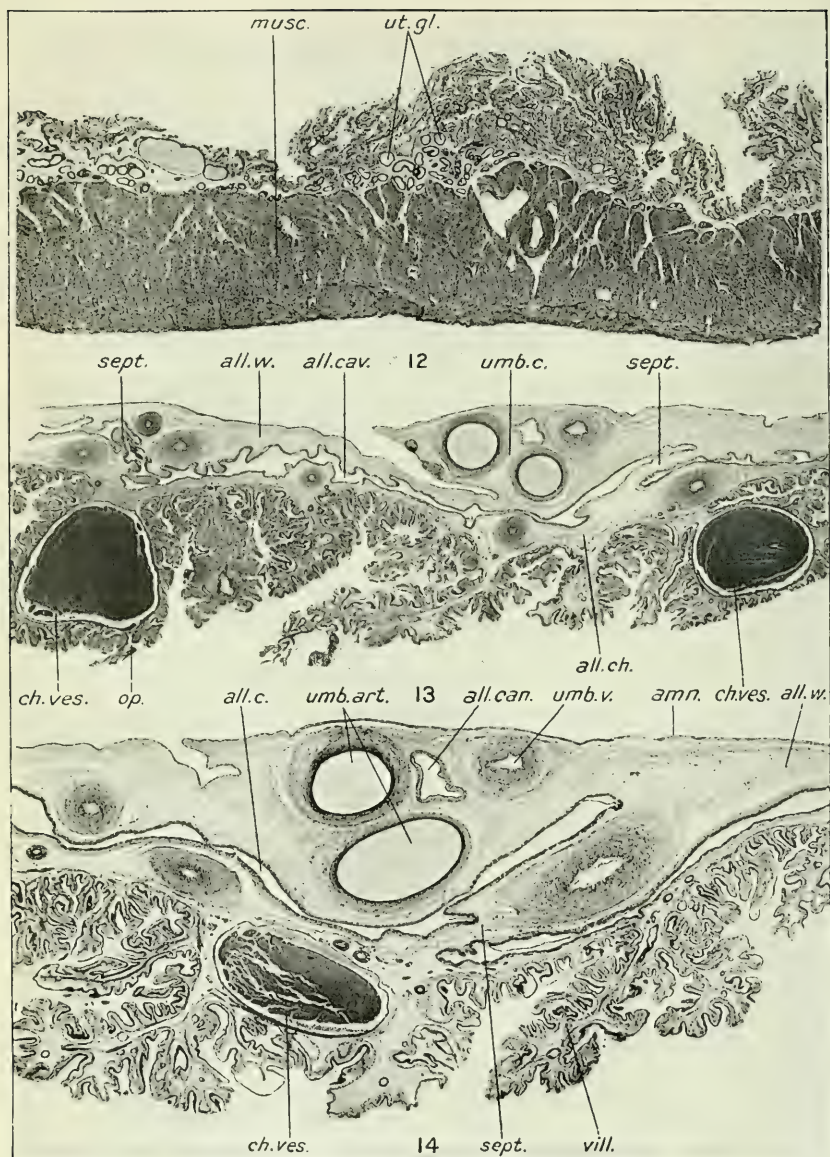
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10

FETAL MEMBRANES OF *CHIROMYS MADAGASCARIENSIS*.

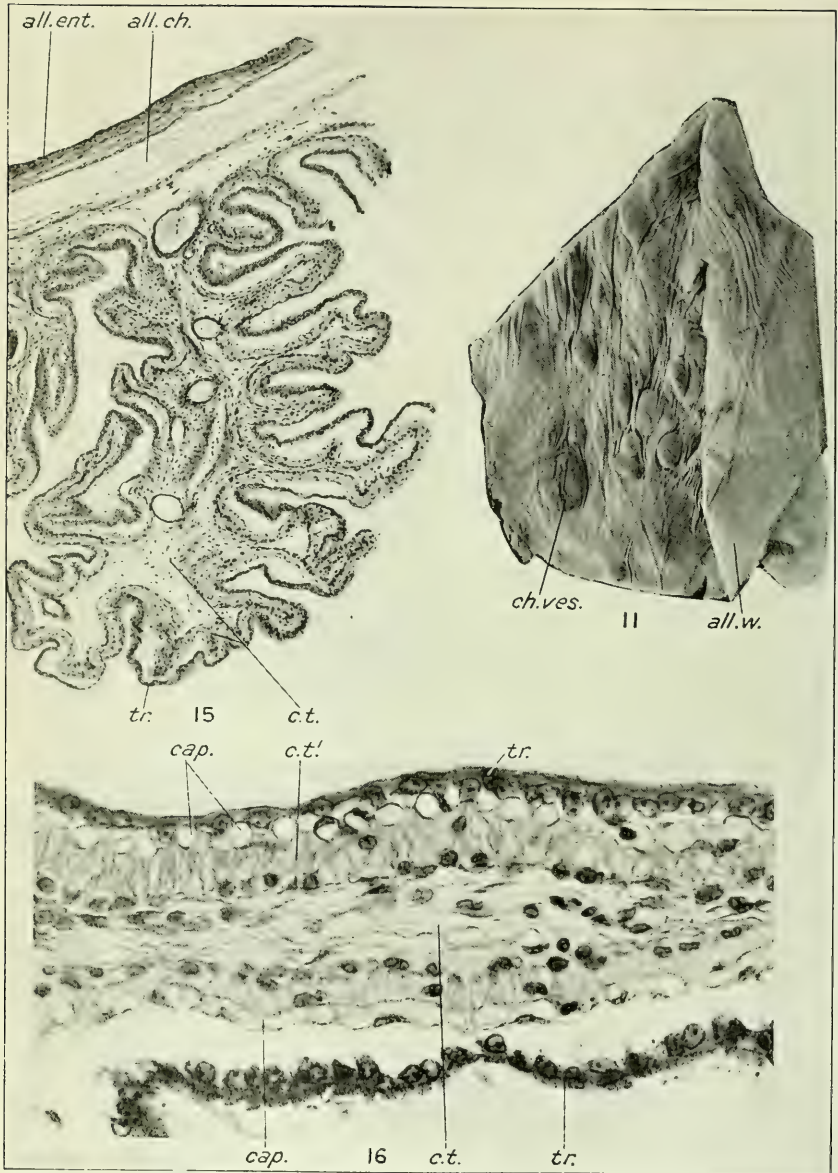




FETAL MEMBRANES OF *CHIROMYS MADAGASCARIENSIS*.







FÆTAL MEMBRANES OF *CHIROMYS MADAGASCARIENSIS*.

51. The Fœtal Membranes and Placentation of *Chiromys madagascariensis*. By Professor J. P. HILL, F.R.S., and R. H. BURNE, M.A. (With an Appendix on the External Characters of the Fœtus, by R. I. Pocock, F.R.S.)

[Received October 24, 1922: Read October 24, 1922.]

(Plates I.—VI.\*; Text-figures 1–6.)

The structure of the fœtal membranes and placenta of the Lemurs was first made known during the years 1871–1877 by the researches of A. Milne Edwards (1, 2, 3) and Sir William Turner (5, 6). Contrary to the prevailing belief, the placenta was shown to be of the non-deciduate diffuse type, quite unlike that of the Apes and Man, and more nearly resembling that of certain Ungulates, particularly the Pigs.

The species examined at that time belonged exclusively to the subfamilies *Lemurinae* and *Indrisinae*, of Madagascar, but in 1884 a brief description of the fœtal membranes of the remarkable Madagascar Lemur, *Chiromys*, was published by Milne Edwards (4), and twenty-five years later Hubrecht (10) reproduced a photograph of the surface of the chorion of a fœtal specimen of the same in the collection of the British Museum and now in our possession (our specimen B).

In 1894 our knowledge, hitherto confined to the Madagascar species of the order, was extended to the Lemurs of the Old World by the preliminary description by Hubrecht (8) of pregnant uteri of *Nycticebus tardigradus* and *Tarsius spectrum*. He showed that in the first-named species the placenta conformed, with some minor though characteristic differences, to that of the Madagascar Lemurs, but that the placenta of *Tarsius* was quite different, and resembled that of the Apes and Man in being discoidal and deciduate. In a later paper (9) Hubrecht gave a more detailed account of the development of the placenta of *Tarsius*, but no further description of that of *Nycticebus* has appeared. In 1902, however, our knowledge of the placentation of the Lorisiformes was further extended by the publication of a lengthy paper by Strahl (14) on the placenta of the African genus *Galago*, wherein it is shown that *Galago*, in the details of its placentation, agrees more closely with *Nycticebus* than with the Madagascar Lemurs, as was to be expected. Strahl in a subsequent paper (15) and more recently Jenkinson (16) have added to our knowledge more especially of the histology of the placenta of these latter forms.

The fœtal membranes and placentation have now been described in more or less detail in representatives of all the existing families and subfamilies of the two groups of the true Lemurs—

\* For explanation of the Plates, see p. 1169.

the Lemuriformes and the Lorisiformes\*, and as the outcome, we know that all the true Lemurs are characterized by the possession of the same non-deciduate, diffuse, epithelio-chorial type of placenta, which differs in the two groups and from genus to genus only in comparatively unimportant though apparently quite characteristic details, the general nature of which is indicated in the following paragraphs (*cf.* also 17).

Development is of the central type, and the entire mucosa of the bicornuate uterus is involved in placental formation; for, though development begins in one of the uterine horns, and the foetus, invested in its membranes, later occupies both that and the body of the uterus, the chorionic sac sends a prolongation, at any rate during the later stages of pregnancy (Milne-Edwards, 3; Turner, 5; Anthony, 12), also into the unoccupied or non-foetal horn, forming what we shall speak of as the chorionic appendage. The uterine epithelium, immediately below which are richly developed maternal capillaries, persists throughout the gestation period, and is regarded both by Turner (5) and Strahl (14) as being actively secretory. The uterine glands also persist in an active functional condition. They mostly open in groups in localised bare areas in the Lemuriformes (Milne-Edwards, 3; Turner, 5; Strahl, 15), and in *Galago* among the Lorisiformes (Strahl, 14), or their openings are more evenly distributed at the bottom of the uterine crypts, as in *Nycticebus* (Hubrecht, 8). The mucosa is always more or less markedly folded, the villous outgrowths of the chorion fitting into the depressions or crypts between the folds.

The chorion is early established as a complete bilaminar membrane enclosing the embryonal formation, and becomes secondarily vascularised by the umbilical (allantoic) vessels as the result of the early fusion of the outer wall of the allantois with its inner surface. The chorion in this way is converted into an allanto-chorion over the greater part of its extent. The allantois is voluminous and multilobulate, covering the greater part of the inner surface of the chorion; and in later stages the amnion is fused with its inner wall, the extra-embryonal coelom being obliterated. The yolk-sac is early separated off as a complete vesicle, appearing in later stages as a quite small flattened sac (Milne Edwards, 3 & 4; Strahl, 14).

The chorion, except over certain small restricted areas and at its vaginal extremity, is produced into villous processes, which amongst the Lemuriformes take the form of large laminar or leaf-like folds, secondarily branched, or amongst the Lorisiformes, of nodular processes. They are covered by a simple layer of trophoblast (tropho-ectoderm), below which is a richly developed plexus of allantoic capillaries. These villous outgrowths fit into complementary depressions of the folded surface of the mucosa,

\* See our reference list, in which the species studied have been noted under the names of the investigators.



the placental connection being constituted by the close inter-digitation of the vascular villous processes of the foetal chorion with the vascular folds of the uterine mucosa or maternal decidua. There is no organic continuity between the two, and at birth the villous processes are simply withdrawn from their mucosal pockets, there being apparently no loss of maternal tissue—i.e., the placentation is non-deciduate.

The secretion of the uterine glands is of high importance for the nutrition of the foetus, and in the *Lorisiformes* there are present pockets or recesses of the chorion (chorionic recesses, Hubrecht, 8; chorionic vesicles, Strahl, 14) specially adapted for its collection and absorption, their openings in *Galago* lying opposite the depressed bare areas on which the uterine glands open (Strahl, 14). Corresponding bare areas of the chorion, in contiguity with uterine bare areas, would seem to subserve the same function in the *Lemuriformes*, though chorionic vesicles of simple structure are, we find, present in *Chiromys* and seem also to occur in *Lemur mongoz* (Strahl, 15).

Notwithstanding the extent of our knowledge of the placentation of the Lemurs, and the fact that in essentials the foetal membranes and placenta of *Chiromys* are similar to those of other Madagascar forms, we offer no apology for presenting yet another contribution to this subject, since the aberrant nature and great rarity of the species make it desirable that these structures should be described and figured more fully than has been done in the papers (4) and (10) referred to above.

The following account is based on the examination of two uteri in a late and almost identical stage of pregnancy. Both foetuses appear to be near full term, and are practically fully haired with the eyelids open. The external characters of the foetus (Specimen B, Pl. III. fig. 6) are described by Mr. R. I. Pocock in the Appendix to this paper.

Specimen A\* was obtained from a female purchased several years ago by the Royal College of Surgeons from Mr. J. Hamlyn. The hinder part of the body was removed, and the uterus preserved *in situ* in alcohol.

Specimen B was originally in the collection of the British Museum. In 1921 it was received in exchange by one of us (H.) through the kind offices of Mr. Oldfield Thomas. According to the label accompanying the specimen, it was purchased of Mr. Stevens on October 1st, 1864. The uterus which accompanied the specimen was strongly contracted, from which we judge that it had been opened in the fresh state and, after extraction of the foetus enclosed in its membranes, had been with the latter at once plunged into spirit. Apart from the partial separation and disappearance in places of the superficial epithelial layers, the foetal membranes and uterus prove to be remarkably well preserved. This specimen formed the

\* R. Coll. Surg. Museum, Physiol. Series, Nos. 3582.5, 3582.51, 3582.52.

subject of Hubrecht's brief reference and figure (10, p. 115 & fig. 151).

For comparison with our preparations of *Chiromys*, we have had available some sections of the placenta of *Nycticebus* from the collection of the late Dr. R. Assheton, kindly placed at the disposal of one of us by Mrs. Assheton, and also preparations made from the imbedded material of *Lepilemur*, which formed the subject of the contribution of the late Dr. J. W. Jenkinson (16), for the use of which we are much indebted to Prof. E. S. Goodrich, F.R.S.

#### UTERUS.

The uterus (specimen A, Pl. I. fig. 1) is much dilated, and forms a pear-shaped mass about the size and figure of a small clenched fist, continuous with the vagina posteriorly by a short narrow cervical segment. Its convex anterior end projects forward further on the left than on the right, and is indented to the right of the mid-line by a shallow vertical furrow, which marks the division between the two unequally dilated horns. Internally this division is emphasised by the projection of a semi-lunar fold (Pl. I. fig. 1, *fld.*) from the line of the external furrow for some 2 or 3 cm. into the uterine cavity.

From the side of each horn, a short distance posterior to its fundus, projects a fold of the broad ligament carrying the contorted Fallopian tube, and by its reflexion forming a deep peritoneal pouch, within which lies the ovary attached by a long ovarian ligament to the uterus. About 1 cm. ventral to the termination of the Fallopian tube is the commencement of the round ligament whence the ligament passes to the groin in a fold projecting freely from the surface of the broad ligament.

In specimen B, owing to strong contraction during preservation, it is probable that the shape of the uterus is to some extent unnatural. It is transversely extended, being nearly twice as broad (at the level of the Fallopian tubes) as the distance between its cervix and fundus. The left horn is considerably more dilated than the right, and forms a rounded bulbous extension of the corpus uteri, with the entry of the Fallopian tube placed some distance behind its anterior margin. The right horn is much smaller with a conical apex to which is attached the Fallopian tube. The union of the two horns is not indicated externally by a furrow as in specimen A, but upon the antero-ventral surface the position of the internal fold that separates them is marked by a slight ridge.

The uterus (specimen A) when opened along its posterior (dorsal) aspect was found to be completely filled both as regards cornua, corpus, and cervix by the foetal membranes (Pl. I. fig. 1), the well-marked chorionic appendage occupying the right cornu, and a prolongation of the main sac extending into the cervical canal (Pl. I. fig. 1, *p.*). Within them lay the foetus, far advanced



in development, occupying the left horn and corpus uteri, with its back turned to the right and presenting with the head.

This position of the fœtus is that generally found in Lemurs towards the end of gestation, though sometimes the fœtus may be in the right horn and corpus uteri (Anthony, 12, p. 247; Turner, 5, p. 574), and sometimes may offer a breech presentation (Turner, 5, p. 573 & 7, p. 278) or may lie diagonally (Turner, 5, p. 574).

In specimen B, so far as we can judge, the elongate embryonal formation lay disposed transversely in the uterus, with the head-end of the fœtus in the corpus uteri, directed to the right, its thicker remainder occupying the more extensive left portion of the corpus uteri as well as the left cornu, whilst the chorionic appendage (Pls. III., IV. figs. 5 & 7) projected into the right cornu. The mid-region of the back of the fœtus would thus lie closely apposed to the internal os uteri, in a position somewhat similar to that occupied by one of Turner's specimens of *Lemur rufipes* (5, p. 574).

The wall of the uterus in specimen A is comparatively thin. Its mucous lining (except within the cervix and around the internal os where it is smooth) is thrown into irregular anastomosing folds with intervening depressions, within which are received the villous folds which project from the chorion. The general correspondence between the mucosal folds and depressions on the one hand and the laminar villous folds and the clefts between them on the other is clearly apparent in Pl. I. fig. 1, and though both sets of folds are somewhat shrunken, there was clear evidence of close interdigitation between the two.

In specimen A, the cervix was occupied, as mentioned above, by a conical smooth prolongation of the chorion, but in specimen B the fetal membranes did not extend beyond the os internum, and the cervix was empty and produced internally into longitudinal folds. The os externum in B projected freely into the vagina and possessed a lobed margin. In A, it was in addition guarded by two semi-lunar folds, projecting from the wall of the vagina, as in the unimpregnated state\*. The cervical canal in neither case showed any indication of being closed, as in the human subject, by a plug of secretion.

In specimen B, the mucosa reaches its maximum thickness in the right cornu, and its folds are here more markedly developed than elsewhere in the uterus, in correspondence with the strong development of the laminar villi on the chorionic appendage. Round the internal os, as in A, the mucosa is relatively smooth.

A low-power view of a section through the body of the uterus (specimen B) is reproduced in Pl. V. fig. 12. The muscularis (*musc.*) though thin relatively to the size of the uterus, is well developed, and in sections in the appropriate plane is seen to consist of an outer slightly thicker layer of longitudinal smooth muscle

\* R. Coll. Surg. Museum, Physiol. Series, No. 2815 A.

and an inner thinner layer of circular fibres; between the two layers there are situated the main branches of the uterine vessels. In the muscularis there are present numerous endothelially lined cleft-like lymphatic channels.

In the intervals between its much subdivided folds the mucosa appears as a relatively thin layer, well supplied with vessels. Over much of its surface the uterine epithelium has separated in our material, but in places it is quite well preserved. It consists of a single layer of, for the most part, relatively large and plump cubical cells with active looking oval or spherical nuclei (text-fig. 1), though here and there the cells are narrow columnar or even flattened and plate-like. It varies in thickness from  $\cdot 016$  to  $\cdot 008$  mm. Whilst its free surface tends to be smooth and regular, its deep surface, in the absence of a basement membrane, is wavy and irregular, the basal ends of its cells being directly applied to the walls of the subjacent capillaries which, as Milne Edwards (3) and Turner (5) have shown, form a richly developed subepithelial plexus. Both Turner (5) and Strahl (15) have maintained that the uterine epithelium is actively secretory,

Text-figure 1.



Section uterine epithelium and underlying capillaries.

but of that we have no positive evidence in our material. Lymphoid exudation no doubt plays a considerable rôle in the nutrition of the fœtus, and it is quite likely that the uterine epithelium is concerned in its transference to the trophoblast cells.

The uterine glands (Pl. V. fig. 12, *ut.gl.*) are mainly confined to the basal part of the mucosa, though not infrequently they are found extending far out in the folds. They show a distinct tendency to be arranged in groups separated by regions in which they are sparse or absent, but we have not been able to determine if they open together, on restricted bare areas as described for other Madagascar Lemurs by Milne Edwards (3), Turner (5), and Strahl (15). We have not been able to distinguish such areas in surface examination of the mucosa, and in the sections the glands are seen to open between the bases of the folds by way of duct-like involutions of the uterine epithelium.

The glands are most numerous in the thick mucosa of the right horn, and are for the most part of relatively small diameter ( $\cdot 048$ – $\cdot 12$  mm.), though some are much thicker (up to  $\cdot 35$  mm.).

The glands are lined by a single layer of low columnar cells with spherical deeply staining nuclei in their basal halves, and are actively secretory, the secretion appearing in the gland

lumina as small homogeneous spherules and as a deeply staining coagulum. Where the glands are enlarged and not actively secreting, the lining cells are cubical. In *Lepilemur* the glands are very similar to those of *Chiromys*, but we have observed distinct evidence of branching. Jenkinson (16) states that they "open at the base of depressions"; we find that in this species the localised areas on which the glands open may or may not be depressed, and that they are characterised by the marked thickening and folding of the uterine epithelium. These areas are situated opposite specially thickened patches of the chorionic trophoblast, to which we shall later make reference. In *Nycticebus* the glands are larger than in *Chiromys*, but are otherwise similar. Hubrecht (8) states that they open on the bottoms of the crypts in which the villi are situated. In *Galago* they open, according to Strahl (14), partly on depressed bare areas in relation with chorionic vesicles, partly (in the main horn) independently (p. 193). Strahl is of opinion that in *Galago* extravasated blood in the mucosa is taken up by the uterine gland cells, and is utilised for the nutrition of the fœtus. In none of the material we have examined (*Chiromys*, *Lepilemur*, *Nycticebus*) have we seen any trace of extravasated blood in the corium of the mucosa, though the later is richly supplied with vessels.

## FETAL MEMBRANES.

### 1. *Allanto-chorion*.

The allanto-chorion, or chorion as we may term it for brevity (Pl. I. fig. 1), forms an exact cast of the interior of the uterus, extending from the apex of one horn to the apex of the other, filling the entire corpus uteri and prolonged (in specimen A) by a blunt conical process into the cervix as far as the os externum. Its surface is covered almost all over by characteristic villous outgrowths in the form of more or less broad swollen pleats marked superficially by delicate sinuous convolutions, presenting an appearance as nearly as possible similar to the figure given by Strahl (15, pl. 36. figs. 4 & 5) of the chorion of a 30-mm. fœtus of *Propithecus*. The surface of the folds thus appears to be less elaborated than in the Lemurs described by Turner (5, p. 575 & 7, p. 279) or in the later stages of *Propithecus* (Strahl, 15, p. 273). The primary pleats are set for the most part transversely to the length of the chorionic sac, becoming more regularly disposed in each horn in parallel circular wreath-like bands.

In specimen B (Pls. III., IV. figs. 4, 5, & 7-10), the laminar arrangement is in parts masked to some extent by the depth of the secondary foldings which break up the primary pleats and produce a more lobulated surface than in the specimen A (Pl. IV. fig. 9). This lobulation must not be confused with the appearance presented by the characteristic polygonal villi of the genus *Nycticebus*

(Hubrecht, 8, p. 93), nor with that of the somewhat similar villi of *Galago* (Strahl, 14 & 15, pl. 38. fig. 17); it is simply a slight elaboration, such as that described by Strahl in the later stages of *Propithecus*, of the laminar arrangement typical of all the Madagascar species.

In opening the uterus of specimen A, it was observed that the folds and corrugations upon the surface of the chorion fit closely into the corresponding depressions in the uterine mucosa. The connection between the two is, however, relatively slight, and by gentle traction the chorionic sac can be detached from the uterus without rupture of tissue. The degree of cohesion between the two differs in different parts, depending on the size and complication of the folds and the depth to which they interdigitate with the corresponding irregularities of the uterine mucosa, being greatest in the non-fœtal (right) horn, where the chorionic folds are most pronounced (Pl. I. fig. 1) and least towards the cervix, where they are fewer and less prominent.

Although, as mentioned above, the folds cover most parts of the chorion, there are areas from which they are almost or entirely absent (Pl. I. fig. 1). Such bare places are very ill-defined, and although at first sight they suggest the bare patches described by Milne Edwards (3) and Turner (5), and figured by Strahl for *Propithecus* (15, pl. 37. fig. 14), they can hardly bear a strict comparison with them. In the first place, they are in every way so much less definite and in the second place, they have apparently no uterine counterpart in the form of bare areas of the mucosa.

The position of these relatively bare areas is no more definite than their boundaries; some can be observed towards the base of the left (fœtal) horn and in the region of the corpus uteri, more particularly towards the cervix where the chorionic folds become smaller and less numerous than elsewhere and ultimately vanish, leaving the conical process of the chorion that occupies the cervix perfectly smooth. In this complete absence of folds at the posterior extremity of the chorionic sac in specimen A, the placenta conforms to the type "placenta en cloche," as originally described in *Propithecus* by Milne Edwards (1).

The chorionic sac of specimen B was figured by Hubrecht (10, pl. GG, fig. 151). It had been opened dorsally from a point opposite the lumbar region of the fœtus to the head. In all essential features it resembles that of specimen A. The laminar folds are fairly evenly distributed upon the surface of the sac opposite the right side of the fœtus (Pl. III. fig. 4); they are closely crowded together, and are arranged for the most part transversely to its long axis. Towards the hinder end they become (as in specimen A) less continuous and less closely packed than further forward, and show four areas apparently bare, but in reality covered with fine ridges and grooves, giving an appearance of fine striation (Pls. III., IV. figs. 4 & 10). Opposite the left side of the fœtus (Pls. III., IV. figs. 5 & 7) is the process or appendage, as



we term it, of the chorionic sac that occupied the right horn of the uterus. Upon its surface the chorionic folds reach their maximum (as in specimen A), and display strongly marked secondary folds and convolutions (Pl. IV. figs. 7, 8, & 9). Elsewhere upon this face of the chorion, and more particularly opposite the head of the fœtus, the folds are relatively weak, and form low ridges separated by wide smooth areas; similar bare places also occur opposite the postero-dorsal aspect of the fœtus.

In comparison with the condition of the chorion in other Madagascar Lemurs, the strong lamination of the appendage that occupies the right (non-fœtal) horn of the uterus is worthy of notice. This prolongation of the chorionic sac may be absent even at near full term (Anthony, 12, p. 247, *Propithecus*), and apparently, as a rule, enters the non-fœtal horn only as pregnancy advances (Turner, 5, pp. 578, 587; Anthony, 12, p. 247), and is normally less strongly laminated than other parts of the sac.

## 2. Allantois.

The allantois, as in other Lemurs, is a voluminous and characteristically lobulated organ whose cavity, though extensive in the circumferential plane, is flattened radially between the chorion with which its outer wall is fused and the amnion which is fused with its inner wall. Between the entodermal lining of the allantoic sac and the trophoblast of the chorion is situated a layer of delicate fibrillar connective tissue, formed from the allanto-chorionic mesenchyme and prolonged to form the axes of the villous folds. In it run the numerous branches and factors of the allantoic arteries and vein on their way to and from the subtrophoblastic capillary plexus, presently to be described.

The allantois consists of a main lobe, into which the allantoic canal opens and which accordingly represents the primitive allantoic vesicle, and of a number of accessory lobes of irregular shape, which have grown out from the primary sac and approach one another across the rump and back of the fœtus. In specimen A the relations of the main sac and its various lobes to the underlying fœtus were ascertained by carefully dissecting away the chorion. Two views of the preparation\* so made are shown in Pl. II. figs. 2 and 3 (*cf.* also text-figs. 2 & 3), representing the left and right sides respectively of the fœtus.

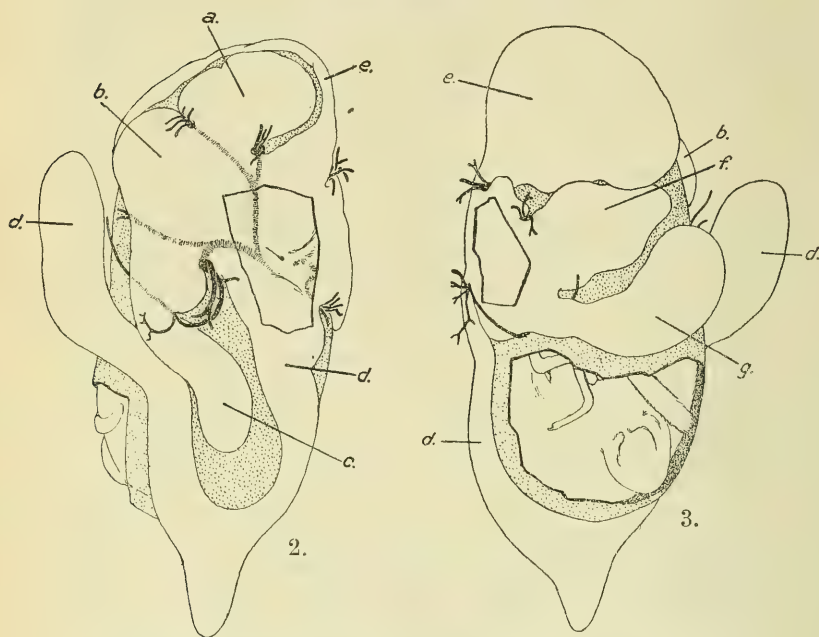
The main lobe (partially opened in text-figs. 2 & 3 and Pl. II. figs. 2 & 3) lies upon the left side of the posterior trunk region of the fœtus, and extends across the ventral surface some little way beyond the mid-line on to the right side, covering the feet and tail. It communicates with the allantoic canal, which runs down in the umbilical cord, by a small slit-like aperture, situated opposite the gap between the left knee and elbow.

\* R. Coll. Surgeons Museum, Physiol. Series, No. 3582.52.



From the dorsal margin of the main cavity three accessory lobes stretch across the left aspect of the fœtus (text-fig. 2 and Pl. II. fig. 2): (*a*) a posterior lobe that runs caudally nearly to the mid-line of the amniotic sac; (*b*) a dorsal lobe that covers the flank and sacral regions of the fœtus and extends for a short distance beyond the dorsal mid-line; (*c*) a cephalic lobe, of sausage-shape, that passes directly towards the head of the fœtus across the shoulder as far as the root of the left ear. At the base of this lobe is a small ventrally directed subsidiary pocket.

Text-figures 2 &amp; 3.



Spec. A, from left and right sides respectively, of fœtus, after removal of chorion, to show the main and accessory lobes of allantois.

The cephalic margin of the main cavity gives rise to but one lobule (*d*), an extensive finger-shaped sac folded back upon itself in the form, roughly, of a Y. The sac runs at first cephalad across the left eye of the fœtus, and then is reflected round the cephalic pole of the amniotic sac, giving off at its furthest point a blunt conical process (the tail of the Y) that extends into the similarly shaped prolongation of the chorionic sac that occupies the cervix uteri. After thus curving round the cephalic pole of the amnion, the lobule *d* passes caudad along the dorsal surface

of the foetus, and leaving the amnion extends into and fills the chorionic appendage that lies within the unoccupied right horn of the uterus. Turner (5, p. 577) states that in *L. rufipes* the allantois does not extend into "the short diverticulum of the chorion which occupies the non-gravid horn." In specimen B we find a similar condition. The terminal process of the lobule extended to the mouth of the chorionic appendage and fitted closely within its lip, but did not project further into its cavity.

From the ventro-caudal margin of the main cavity arises a lobe (*e*) that curves round the ventral surface of the caudal end of the foetus, covering the root of the tail and the right hind limb and reaching to within a short distance of the free margins of lobes *a* and *b*.

Upon the right side of the foetus (Pl. II. fig. 3 and text-fig. 3) the main cavity gives off from its dorsal border two lobes (*f* and *g*) that pass towards the dorsal mid-line across the lumbar and thoracic regions of the foetus. The caudal of these extends rather more than half-way towards the mid-line of the back; the other (*g*) is a larger, sausage-shaped sac, that dilates gradually from a comparatively narrow origin to a bluntly rounded extremity and terminates upon the back of the foetus in contact with lobe *d*, at the point at which the latter leaves the amnion to enter the appendage of the chorion.

Apart from the narrowness of the commencement of this lobe, there is no indication in the allantois of the pedunculated subsidiary lobes mentioned by Milne Edwards (3) as occurring in *Propithecus*.

The umbilical cord was exposed in specimen B (Pl. III. fig. 6). It measured 4.3 cm. in length, and at its emergence from the body of the foetus was subcylindrical. At about the middle of its length it became more flattened, appearing as a ribbon-like band, some 6 mm. in width, bordered on each side by a thinner selva. It joined the inner wall of the main allantoic lobe over the right latero-dorsal surface of the foetus, running, attached to the wall, for a distance of about 1.5 cm. before finally disappearing. In specimen A, the cord passed to the left side of the foetus to reach the main lobe.

The cord (Pl. V. figs. 13, *umb.c.*, & 14) consists of a connective-tissue matrix, in which are situated the allantoic canal and the umbilical vessels. It is invested by the amnion, the epithelial layer of which is quite thin, resembling in places a cuticular membrane, and below this is a thin layer of connective tissue, rich in cells and not everywhere clearly marked off from the connective tissue of the cord. The allantoic canal (*all.can.*), situated between the vessels, possesses a wide lumen, lined by a two-layered epithelium of the transitional type. There are three umbilical vessels, two arteries, and one vein. The two arteries (Pl. V. fig. 14, *umb.art.*) contain blood, and their walls are histologically similar, each possessing a compact zone of smooth muscle just outside the

lining endothelium. The vein (fig. 14, *umb.v.*) is empty, and its wall lacks the compact zone of muscle and appears contracted and its lining folded.

Epithelial pearls occur below the amniotic investment of the cord in the region of its junction with the allantoic sac, and are probably derived from the amniotic epithelium, since they are also occasionally found below the amnion covering the inner wall of the allantois adjacent to the cord-junction.

From the junctional region, branches of the umbilical vessels pass off to run in the inner wall of the main allantoic sac. Some of these after a short course reach the allanto-chorionic connective tissue directly in specimen B, by way of three septal pillars (figs. 13 & 14, *sept.*) which extend obliquely across the lumen of the main sac between its inner and outer walls, as Strahl appears to have observed in *Galago* (14, p. 182). In specimen A, these septa appear to be absent. Other branches after a straight or slightly branched course reach the allanto-chorion by passing round the margin of the main sac. They are seen emerging in Pl. II. figs. 2 & 3 and text-figs. 2 & 3 in the angles of the clefts between the main and accessory lobes. Yet other branches run straight on from the inner wall of the main sac to supply those regions of the chorion that are not underlain by prolongations of the allantois. In the chorionic connective tissue, the vessels subdivide and run in all directions to supply the subtrophoblastic capillary plexus of the laminar villi.

Both Milne Edwards (3) and Anthony (12) state that the allantoic walls in the Lemurs examined by them are devoid of blood-vessels. That, of course, is an erroneous statement as applied to the allantois as a whole, but it is partially true of the accessory lobes, since the inner walls of these (remarkably delicate and thin, as Milne Edwards remarks) are quite devoid of vessels. Thus it is an unexpected and somewhat remarkable fact that these accessory allantoic lobes in the Lemurs are not really concerned with the vascularization of the chorion, and the question arises as to their possible significance. One of the functions of the allantois is to serve as a receptacle for the urinary fluid excreted by the mesonephroi, and it is possible that the formation of these lobes is to be correlated with the presence in the fœtus of actively functional mesonephroi. In this connection it is interesting to note that Hubrecht (11) records that in the 6-mm. embryo of *Nycticebus*, the glomeruli of the mesonephros are remarkably large.

Whatever may have been the inciting cause of the growth of the allantois, there can be little doubt that its lobulated form is, as Milne Edwards (3, p. 283) suggested, a direct result of the position early assumed by the umbilical vessels on the walls of the main lobe, the first formed part of the organ. If that be so, then the actual form assumed by the allantois is a secondary matter and likely to be inconstant in its details, even in the

individuals of the same age. From Milne Edwards's observations we know that in younger specimens it is simpler than in older.

It should be noted that the main sac and its lobes do not completely clothe the inner surface of the chorion (text-figs. 2 & 3), there being left between the lobes considerable areas where the amnion is fused directly with the inner surface of that membrane.

The entodermal lining of the allantois is formed by a well-marked cubical epithelium, quite different from that lining the allantoic canal. Its inner surface is not everywhere smooth, but is produced into low folds, more numerous in the main sac than in the accessory lobes. Its mesodermal wall is relatively thin, and consists of fibrillar connective tissue, dense just outside the entodermal lining, but delicate and loose elsewhere both in the inner and outer walls. In parts it is reticular in character. It is rich in cells both fixed and migratory.

### 3. *Yolk-sac.*

We have not found any definite traces of the yolk-stalk and yolk-sac in our specimens, unless an irregular epithelial strand in process of cornification, which is situated below the amnion of the umbilical cord in the region of junction and bounded on its inner side by a mass of gelatinous connective tissue, represents the degenerate remains of the stalk. Milne Edwards (3) figures the yolk-sac in relatively late fœtuses of *Propithecus diadema* and *Indris brevicaudatus* (v. especially his pl. 120, where in a late but not yet haired fœtus of the latter species it is shown as a quite small, flattened, and stalked vesicle, situated towards the distal extremity of the allantoic stalk—i. e., approximately in the position of our cornifying strand). Strahl (14) simply mentions that in a 36-mm. fœtus of *Galago* the yolk-sac is "gut nachweisbar." Jenkinson (16) states that in *Lepilemur* "no trace of the yolk-sac was found."

### 4. *Amnion.*

The amnion forms an oval sac fitting loosely around the fœtus. It invests the umbilical cord throughout its length, and at the distal extremity of that spreads out to become loosely fused with the inner wall of the allantoic sac and its lobes. In the intervals between the latter it is fused directly with the connective tissue of the chorion. The most extensive areas of the amnion that are in this way in direct apposition and fusion with the chorion lie towards the head-end of the fœtus (text-figs. 2 & 3 and Pl. II. figs. 2 & 3). There is an extensive area covering the whole of the right side of the head and shoulders (text-fig. 3), and narrower patches over the left side of the head and shoulders (text-fig. 2) and along the back between the apices of the allantoic lobes. As in the higher Primates, the expansion of the amniotic sac and its adherence to the inner wall of the allantois have brought about the complete obliteration of the extra-embryonal cœlom.



*Minute Structure of the Allantoic Chorion and its Villi.*

The general appearance of the chorion and its villi in section is illustrated in Pls. V., VI. figs. 13, 14, and 15.

The allanto-chorion consists essentially of the outer wall of the allantois fused with the chorion proper. It thus comprises the following layers:—(1) the allantoic endoderm; (2) the composite allanto-chorionic connective tissue which is continued out to form the cores of the complexly folded laminar villi, and in which are situated the branches of the umbilical vessels; (3) the superficial covering of trophoblast (tropho-ectoderm, chorionic ectoderm).

The trophoblast (fig. 16, *tr.*) throughout its extent is singularly uniform in character, varying only in thickness, and that with no apparent regularity, though frequently it is thinned in places over the apices of the villous branches. It attains a maximum thickness of .024 mm. and a minimum of .005 mm. or even slightly less. Where it is thickest, it consists of a well-defined single layer of cubical cells, with their outer surfaces projecting convexly. The nuclei are large and deeply staining. The cytoplasm of the outer zone of the cell-body is homogeneous or very finely granular and strongly eosinophil; that of the deeper zone below the nucleus is reticular in character, and stains lightly. There is no basement membrane, and the basal ends of the cells rest, just like those of the uterine epithelium, directly on the endothelial walls of the underlying capillaries (fig. 16, *cap.*). These are relatively large and very abundant, forming a richly developed subepithelial plexus, first figured by Milne Edwards from injected specimens of *Propithecus diadema* and *Indris brevicaudatus* (3, pl. 121, figs. 1, 2, & 4). In *Galago* also, according to Strahl (14), the capillary network of the villi lies in direct contact with the epithelial covering.

The mesodermal core of the villi (Pl. VI. fig. 16) is formed by a variety of fibrillar connective tissue, differentiated into two zones: (a) a looser less deeply staining central zone (*c.t.*), containing numerous leucocytes and lymphocytes and in which are situated the smaller branches of the umbilical vessels; and (b) a highly characteristic peripheral zone in the form of a perfectly continuous and more deeply staining layer of uniform thickness which lies immediately below, and evidently forms a support for the subtrophoblastic capillary plexus. This peripheral zone (Pl. VI. fig. 16, *c.t.*) consists of a coarse fibrous reticulum, the stronger fibres of which run out at right angles to the surface, so that under a low power the zone presents a striate appearance, suggestive at first sight of a columnar epithelium, more especially as the nuclei of its cells of origin are mainly arranged in an irregular row, defining the deep surface of the zone. Round the nuclei there is sometimes visible a small amount of cytoplasm, which appears to be directly continuous with the fibrous network. This zone would seem to be distinctive of the villi of *Chiromys*. It is not present either in *Lepilemur* or *Nycticebus*. In both these forms the



trophoblast is very similar to that of *Chiromys*, but in neither of them is the subtrophoblast capillary plexus anything like so well developed, the capillaries being smaller and much less numerous than in *Chiromys*.

We have, unfortunately, no preparations of *Chiromys* which show the relation of the villi to the folds of the uterine mucosa, and are thus unable to state definitely whether the interdigitation of the two was of the same intimate nature as occurs in *Lepilemur* (Jenkinson, 16) and *Propithecus coronatus* (Strahl, 15), or was of a looser character, approximating to the conditions we find in *Nycticebus*. In the latter, Assheton states that "the foetal villi appear to hang in grape-like bunches into the mouths of much wider depressions" (18, p. 269); and the sections certainly suggest that considerable areas of the lateral surfaces of the villi do not come into contact with the uterine folds, and that intimate apposition between the trophoblast and the uterine epithelium is largely limited to the flattened surfaces of the ends of the villi. In this connection it is worthy of note that gland-secretion is present in fair abundance round the proximal portions of the villi. In *Galago*, Strahl (14) states that over the tips (except in the region of the terminal pits) and lateral surfaces of the villi the trophoblast and uterine epithelium are firmly attached to each other, but in the intervillous intervals the connection is less intimate.

In *Lepilemur*, the villi are somewhat similar in character to those of *Chiromys*, but are readily distinguishable therefrom, being much less coarse and more finely branched. The mucosal folds are likewise very thin, as is the case also, according to Strahl (15), in the 60-65-mm. foetal stage of *Propithecus*, whilst their relations to the villous folds are exceedingly intimate. In our sections of *Lepilemur*, the uterine epithelium, practically everywhere in the villous regions, has become separated from the underlying connective tissue of the mucosal folds, and is seen as a relatively thin layer in close and intimate apposition with the thicker, more cubical trophoblast. In *Propithecus*, Strahl (15) also describes the two epithelia as being in close contact. In *Chiromys*, we incline to believe that the relations between uterine epithelium and trophoblast were not throughout quite so intimate as in the two Lemurs just referred to.

#### CHORIONIC VESICLES.

When the deep surface of the allanto-chorion is examined after reflection of the inner wall of the allantois, numbers of small, flattened, ovalish bodies of a reddish-brown colour may be seen embedded in its substance (Pl. VI. fig. 11). These are the chorionic recesses first described and figured by Hubrecht (8) in *Nycticebus*, and later described by Strahl (14) for *Galago*, where he designated them "chorionic vesicles."

These bodies were encountered in both our specimens, but

they were larger and more easily seen in specimen B than in specimen A. They varied considerably in size, the largest measuring  $5.5 \times 4.5$  mm. in diameter, the smallest 1.5 mm. They numbered about sixty, and were chiefly distributed upon the parts of the chorion that overlay the head region of the foetus, being more numerous on the right side than on the left.

In specimen A, although a few of these bodies were as large as in specimen B, the majority were no larger than a pin's head. Most of them were located upon that part of the chorion which occupied the left uterine horn, being particularly numerous upon those areas where the chorionic laminae were most richly developed. Few, if any, could be located with certainty on the chorion within the right horn and the body of the uterus.

In the sections (Pl. V. figs. 13 & 14, *ch.ves.*), the vesicles are seen to be situated either in the allanto-chorionic connective tissue, close to the allantoic lumen, or actually in that of the laminar villi. The vesicle is of simple structure, and unlike those of *Nycticebus* and *Galago*, is devoid of villous folds or ingrowths projecting into its cavity. Its opening is small and slit-like (Pl. V. fig. 13, *op.*). Lining the cavity is a single-layered epithelium, representing an involuted portion of the trophoblast, but differing from that in its characters. It consists of low cubical to flattened cells, .013 to .008 mm. in thickness. The cytoplasm of the cubical cells is reticular in character, and encloses one or more large vacuoles. The nuclei are mostly basal in position, and frequently appear shrunken and irregular. The lining rests on a very thin, compact layer of fibrillar connective tissue. It is noteworthy that the vesicle-wall appears to be entirely devoid of capillaries. The cavity is occupied more or less completely by a coarsely granular coagulum, no doubt representing the secretion of the uterine glands, and in it there occur, here and there, degenerating cells, probably derived from the lining epithelium.

The chorionic vesicles of *Nycticebus* and *Galago* described by Hubrecht and Strahl are more highly differentiated than those of *Chiromys*, and would seem to be specially adapted for the collection and absorption of the secretion of the uterine glands (Strahl, 14). In our sections of *Nycticebus*, we find the vesicle invested externally in a fairly dense fibrous connective-tissue coat, in which there are present numbers of larger and smaller blood-vessels. The lining of the sac is formed by a flattened to cubical epithelium, in contact with the under surface of which there are here and there fair-sized capillaries. The cavity of the vesicle is largely occupied by vascular villi as described by Hubrecht, clothed by an epithelium similar to that lining the cavity, and between the villi is a granular material similar to that found in the uterine glands.

In *Galago*, Strahl (14) described the occurrence of similar vesicles, but found that their openings, unlike those of *Nycticebus*, overlie depressed areas of the mucosa on which are the openings of uterine glands.

In *Chiromys*, the vesicles are evidently not of the same functional importance as in *Nycticebus* and *Galago*, and it may be suggested that they serve not so much as absorptive organs, but rather as reservoirs for the surplus of the uterine-gland secretion which is probably in major part absorbed directly by the trophoblast of the laminar villi.

The general occurrence of chorionic vesicles in the Lemuri-formes has not so far been established. The only reference to their presence that we know of is an inconclusive statement by Strahl-(15) that in *Lemur mongoz*, he observed at one place an indication of a chorionic vesicle devoid of internal villi, overlying a groove in the mucosa which might be a uterine gland area. But what apparently does characterise the chorion of certain of the Madagascar Lemurs, *e. g.* *Propithecus*, is the occurrence of circumscribed chorionic bare patches, opposite which there occur on the mucosa depressed bare areas on which the uterine glands open. Such complementary bare areas (and more especially the uterine) have been described by Milne Edwards and Turner (with excellent figures of the uterine areas, 3, p. 280, and 5, figs. 8 & 9), and more recently by Strahl (15, figs. 14, 15, 16, & 18 *a* & *b*), but none of these observers has given any account of the structure of the chorionic areas, though Turner (5, p. 582) expressly states that "the smooth, non-villous surfaces of the chorion opposite the smooth areas on the mucosa are engaged in the absorption of the secretion of the glands."

In the course of examining our preparations of the late Dr. Jenkinson's material of *Lepilemur*, we observed what we took to be these particular areas; and on referring again to Dr. Jenkinson's paper, we realised that his description (16, p. 180) of the simpler conditions in what he terms "the non-placental [really non-villous] regions," illustrated in his figs. 3-7 and 15, actually refers to the areas which we had identified as the bare areas of previous investigators. As Jenkinson describes, these non-villous areas are characterised by the transformation of the trophoblast covering them, into a thick layer composed of elongated narrow columnar cells, measuring up to .063 mm. in height and just about six times as thick as the normal trophoblast covering the villi (*cf.* Jenkinson's figs. 3, 4, & 5). The cytoplasm of the cells is lightly staining and coarsely reticular in character, and in some of the cells there is a large, clear vacuole situated in the basal part of the cell, below the nucleus. The nuclei are oval and deeply staining, and are situated near the middle of the cell-bodies, though sometimes they approach their free surface. Occasional binucleate cells were observed. Specially characteristic of this epithelium is the production of the outer ends of the cells into bluntly tapering or knob-shaped processes, in which, occasionally, a more or less shrivelled nucleus may be seen. They project into a granular material, "apparently a secretion of the uterine epithelium," according to Jenkinson, and are no doubt absorptive in function. In the basal part of the

layer, there occur at intervals curious spherical cells, and immediately below it, capillaries are present in fair abundance.

The uterine areas, related to the just-described characteristic areas, are more or less folded, and may or may not be depressed. They are characterised by the marked thickening and ridging of the uterine epithelium, and by the presence of the openings of the uterine glands. The uterine epithelium appears as a deeply staining layer, thrown into low ridge-like folds (Jenkinson, fig. 15) and about five times as thick as the ordinary epithelium covering the mucosal folds. It is composed for the most part of narrow columnar or club-shaped cells, with deeply staining cytoplasm and chromatin-rich nuclei. Jenkinson records the presence of goblet cells amongst the ordinary epithelial cells, but we have failed to detect them, and considers the epithelium is secretory. However that may be, and it is probable, coarsely granular material similar to that found in the uterine glands occurs in the interspaces between the thickened trophoblast and the ridged uterine epithelium; and there can be no doubt, we think, that these non-villous chorionic areas have the same functional significance as the chorionic vesicles of the *Lorisiformes*. Indeed, in view of the close adherence of the uterine epithelium to the trophoblast of the chorionic villi, characteristic alike of *Propithecus* (Strahl) and *Lepilemur* (Jenkinson), special absorptive areas in relation to the openings of the uterine glands would seem to be necessary if the secretion of the latter is to be adequately utilised.

It may be noted that these areas attain a relatively considerable size, as may be judged from Strahl's figures of *Propithecus* (15, taf. 37). The largest area we have examined in *Lepilemur* measures over 3 mm. in diameter.

#### CONCLUSION.

In the contribution by one of us (H.) to the discussion on the zoological position and affinities of *Tarsius* (17), the view is expressed (p. 477) that the placentation of the Lemuroids is essentially primitive, "presenting us with a simple little specialised type of placenta from which the more advanced and presumably more efficient arrangements in the other Primates may quite easily have originated as the result of adaptive specialisation in the course of evolution." More detailed acquaintance with the Lemuroid placenta has only served to strengthen us in that conclusion, and has, moreover, entirely failed to reveal the slightest evidence in support of the view expressed by Hubrecht (10, p. 145) and also by Assheton (13, p. 268) that the Lemuroid placenta is a secondarily simplified and derivative type.

These two authorities base their belief very largely on theoretical considerations concerning placental evolution, and consider that the diffuse placenta of the Lemurs is different from that of the Ungulata, Manidæ, Cetacea, etc.



In his speculations on the phylogeny of the placenta, Hubrecht (10) starts out by denying a Reptilian origin for the Mammalia, and postulates a primary phagocytic and absorptive activity on the part of the trophoblast. From the very start of uterine gestation, the trophoblast proliferating rapidly, invaded and destroyed the maternal decidual tissue, and as the result, there was formed a localised placenta of the "deciduate" type in which the maternal blood circulated either in endothelially lined capillaries enclosed by trophoblast (Carnivora, or actually in lacunar spaces in the trophoblast itself (Insectivora, Rodents, etc.). That being the primary and original type of placentation, it follows that all the "diffuse" varieties of placenta in which such phagocytic activity on the part of the trophoblast "was insignificant or absent (Lemurs, certain Edentates, and many Ungulates)" have been derived by simplification from the more elaborate "deciduate" type. Hubrecht admitted, however, that "we cannot for the present indicate the intermediate steps by which the simplification of a placenta of the Insectivorous or Primate type down to that of the present Lemurs was brought about . . ." (10, p. 115); but he saw "no reason why this simplification should not have arisen more than once" (p. 145)—*i.e.*, the diffuse placentation of Lemurs "was not necessarily obtained along the same hereditary line of development" as that of Ungulates. Indeed, he thinks there is sufficient evidence to justify the drawing of a sharp line of distinction between the placentation in these two groups. The late Richard Assheton, in his critique of Hubrecht's monumental paper (10), says (18, p. 268): "I entirely agree with Hubrecht's opinion that the diffuse placentation of the Lemurs is different from that of the true plicate\* forms of Ungulates, Cetacea, some Edentates, etc." Further he writes (p. 265): "Whether the Carnivora or the extreme cumulative or extreme plicate [placenta] is the most primitive, it is very difficult to say"; nevertheless he goes on to suggest that the Lemurine placenta, which he terms "pseudo-plicate," may possibly have been derived by reduction from a cumulate type such as is found in the Carnivora, "by way of such conditions as *Hylobates*, *Semnopithecus*, *Cercocebus*, by the gradual supersession of the glandular activity of the maternal uterus over the phagocytic activity of the foetal trophoblast, and the filling of the blood spaces, into which the foetal villi originally hung, with uterine secretions instead of extravasated maternal blood" (p. 269). But why the Lemurs after having evolved a cumulate (deciduate) placenta should have been under the necessity of substituting for it the plicate (non-deciduate) type is not explained.

\* Assheton suggested a grouping of placental forms based on the behaviour of the trophoblast into (a) Cumulate, characterised by radial, more or less local thickening of the trophoblast which is actively phagocytic (= "Deciduate"); (b) Plicate, characterised by tangential extension and folding of the trophoblast with little or no phagocytic activity (= "Nondeciduate").



We must confess we are quite unable to accept the views of these two authorities, either in respect of the secondary nature of the diffuse placenta of the Lemurs or in regard to its dissimilarity to the diffuse placenta of other Mammals. It appears to us they have attempted to read the story of placental evolution the wrong way round.

In our opinion, any attempt to trace the evolution of mammalian placental arrangements must be based on a consideration of the probable conditions which obtained at the time viviparity replaced oviparity. Knowing the arrangement of the foetal membranes in the existing Monotremes, we can picture the conditions with reasonable certainty. We should postulate, then, that the common ancestral stock, from which the Didelphia and Monodelphia diverged, possessed an arrangement of the foetal membranes similar to that of the existing Monotremes and of *Phascogale* amongst the Marsupials--*i. e.*, the outer wall of the embryonal formation consisted as to one-half or thereabouts of unsplit blastocyst wall or omphalopleure, in part vascularised by the vitelline vessels of the vascular area of the yolk-sac, and as to the remainder, of allanto-chorion, vascularised by the umbilical vessels of the vesicular allantois. The uterine mucosa possessed a persistent covering epithelium, functional uterine glands, and a rich vascular supply.

These being the structural elements involved, the primitive placenta was constituted simply by the close apposition of the omphalopleure and the allanto-chorion with the vascular lining of the uterus. Here we have the simplest possible type of placenta, partly allantoic, partly vitelline and diffuse in the sense that the whole of the outer surface of the embryonal formation is involved in the carrying on of the exchanges between the maternal and foetal blood-streams. The trophoblast covering the entire outer surface is as yet a simple layer, absorptive but not actively phagocytic.

Out of the primitive placenta here outlined, we see no difficulty in deriving on the one hand, the relatively simple placental arrangements characteristic of the Marsupialia and on the other, the varied types of placenta characteristic of the Monodelphia, the non-deciduate diffuse type representing only a relatively slight elaboration of the primitive form, and the varieties of the "deciduate" type resulting from the assumption by the trophoblast of active phagocytic properties, the precise characters assumed by the placenta being in all cases determined by a variety of conditions, intrinsic and environmental or uterine. We therefore remain firm in our belief that the placentation of the Lemurs is genuinely simple and little specialised.

Finally, as concerns the reputed distinction between the Lemuroid diffuse placenta and that of other Mammals, we readily grant there are differences in detail, but we quite fail to see that there is any *fundamental* difference, or even enough difference to justify the calling of the former "pseudo-plicate"

and the latter "plicate." Both are plicate in Assheton's sense, and are characterised on the fœtal side by the presence of a relatively passive trophoblast, markedly folded and of great extent, by the vascularisation of the chorion through a large vesicular allantois and by the reduction of the yolk-sac and its vessels; and on the maternal side, by the persistence of the uterine epithelium (at least in the majority) and of the uterine glands in an active functional condition. In our view, the resemblances far outweigh the differences in detail.

We are accordingly in entire agreement with Jenkinson (16) in believing (1) that the resemblance between the non-deciduate placentation of the Lemuroids and that of other Mammals, *e. g.* the Ungulata, are due to their derivation "from a common ancestral 'indeciduate' type"; and (2) that the deciduate hæmochorial type of placenta characteristic of the other Primates has been evolved from the non-deciduate Lemuroid type, quite independently of that of the Rodents. Insectivora, etc.—another illustration of the principle enunciated by H. F. Osborn that "the *same* results appear independently in descendants of the *same* ancestors."

We are greatly indebted to Mr. F. Pittock for invaluable help in the preparation of Pls. III.—VI. and to Mr. S. Steward for the photographs of Specimen A, Pls. I. & II., and to Mr. Terzi for retouching the same.

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## APPENDIX.

### On the External Characters of a Fœtal *Chiromys*.

By R. I. Pocock, F.R.S.

At the request of the authors, I undertook to examine and describe the external features of the fœtal *Chiromys* (Specimen B, Pl. III. fig. 6), the placenta of which is described in the preceding pages by Prof. Hill and Mr. Burne.

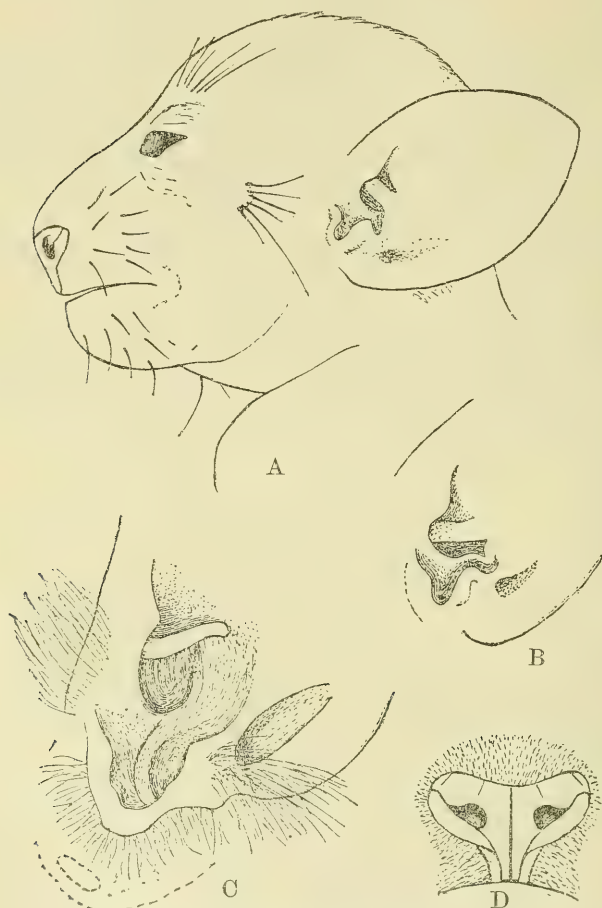
The approximate dimensions in millimetres of the specimen, a male apparently at full time, are as follows:—Dorsal contour length (snout to root of tail) 165; head and body from crown to root of tail 106; head from nose to occiput 37; ear from intertragal notch 21; tail 103; upper arm 25; fore-arm 21; palm of hand 12; thigh 31; lower leg 31; sole of foot 18. The general proportions do not differ greatly from those of the adult, the tail and arm being relatively as long, but the head is relatively larger, the leg shorter, and the digits of the hand shorter than in the adult.

The coat consists of comparatively short and sparse adpressed hairs, brown and grey in colour; on the hands and feet and tail

the tint is blacker; the muzzle and cheeks are nearly naked. In the adult the coat is thick and woolly and black in colour, with long black and white bristles intermixed. The head is relatively larger, and has a more vaulted cranium than in the adult.

The rhinarium is well developed and like that of the adult. So also are the facial vibrissæ, the genal and superciliary tufts

Text-figure 4.



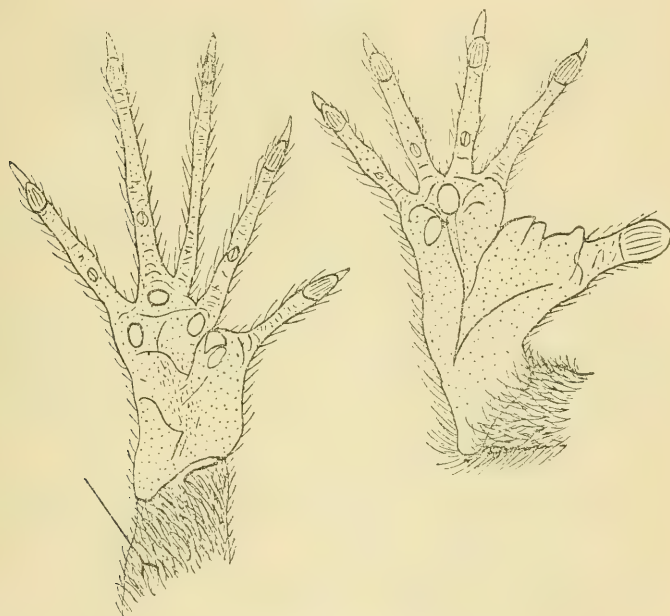
A. Head of fetal *Chiromys*. B. Base of ear of same. C. Base of ear of adult.  
D. Rhinarium of fetal *Chiromys*.

being specially well marked. There is a single interrampal vibrissa. The eyes are much smaller than in the adult, oval and pointed at each end, like the eyes of a diurnal mammal.

The ear is covered with short hair externally, and is flat and not hollowed, but the ridges and depressions characteristic of the adult are all indicated. In the adult the ear is naked internally and deeply hollowed; it is also relatively much larger than in the fœtus, its length being equal to the distance between its intertragal notch and the end of the rhinarium, whereas in the young its length is only equal to the distance from the end of the rhinarium to a point just behind the eye.

The tongue differs in at least two particulars from that of the adult. The distal margin of the sublingua is irregularly pointed and serrulated, and the median inferior ridge ends in a soft straight point, not in a hard down-curved hook. In the points

Text-figure 5.



Hand and foot of fœtal *Chiromys*.

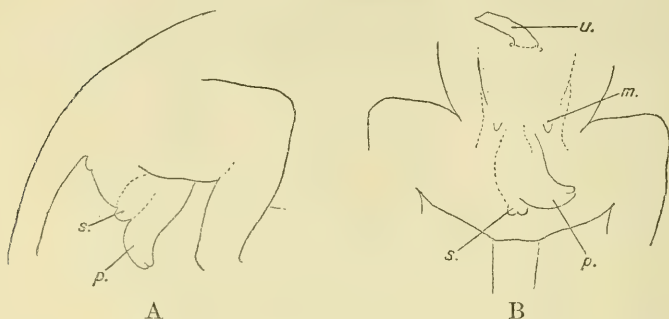
in which the sublingua differs from that of the adult, it approaches the less specialised condition seen in the typical Lemurs.

The fore limbs closely resemble those of the adult, but the digits are relatively much shorter. The fourth digit, for example, is only a little longer than the palm, whereas in the adult it is nearly twice the length. The pollex also is relatively much nearer to the second digit than it is in the adult.

The hind limb closely resembles that of the adult in all important respects. It is, however, relatively shorter in all its parts.

The external genitalia are remarkable for the length and thickness of the penis, the distal end of which is curved forwards, with its posterior, or inferior, surface strongly convex. Proximally it arises in front between the two well-marked inguinal mammæ, and its integument here is mesially grooved. Immediately behind its posterior point of insertion there is a little bilobed thickening of the skin, representing the tip of the

Text-figure 6.



- A. Lateral view of the hind quarters to show the prominence of the penis.  
 B. Ventral view of the hind quarters, with penis turned aside to the left.  
*m.* mamma; *p.* penis; *s.* scrotum; *u.* umbilical cord.

undeveloped scrotum, and above this on each side a shallow groove runs upwards and forwards to the level of the mammæ, apparently defining the inguinal position of the testes. The penis, the inner surfaces of the thighs, and the abdominal region are much more scantily hairy than the upper and outer surfaces of the body and limbs.

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#### EXPLANATION OF THE PLATES.

##### List of Reference Letters.

*all.c.* allantoic cavity; *all.can.* allantoic canal; *all.ch.* allanto-chorion; *all.ent.* allantoic entoderm; *all.w.* inner wall of allantois; *amn.* amnion; *cap.* allantoic capillaries; *ch.a.* chorionic appendage; *ch.ves.* chorionic vesicle; *c.t.* connective tissue of villus; *c.t'.per.* peripheral zone of same; *fld.* fold between uterine cornua; *musc.* muscularis; *op.* opening of chorionic vesicle; *p.* smooth prolongation of chorion into cervix; *sept.* septal pillar between inner and outer walls of allantois; *tr.* trophoblast; *umb.c.* umbilical cord; *umb.art.* umbilical (allantoic) artery; *umb.v.* umbilical vein; *ut.gl.* uterine glands; *vill.* chorionic villus.

Fig. 1. Uterus, *Chiromys*, Spec. A., opened from the dorsal side, showing the chorionic sac *in situ*. The folded character of the mucosa, the chorionic appendage (*ch.a.*) projecting into the right cornu, and the non-villous prolongation (*p.*) into the cervix are well seen. *fld.* fold between uterine cornua. About nat. size.

- Fig. 2. Fœtal *Chiromys*, Spec. A. The chorion has been removed, exposing the main sac of the allantois and its accessory lobes on the left side of fœtus. The head of the fœtus is towards the lower side of the plate. The main sac has been opened up, exposing the opening of the allantoic canal, into which a white rod has been passed. (Cf. text-fig. 2 and text, p. 1153.) Slightly reduced.
- Fig. 3. Fœtal *Chiromys*, Spec. A. The same preparation as in fig. 2, but from the right side of fœtus. An extensive area of the amnion on the right side of the head of the fœtus has been removed. (Cf. text-fig. 3 and text, p. 1155.) Slightly reduced.
- Fig. 4. View of the chorionic sac from the right side of the fœtus, Spec. B, showing the arrangement and character of the laminar villi. The head of the fœtus is towards the left side of the plate. Slightly reduced.
- Fig. 5. Similar view of the left side of the chorionic sac, Spec. B, to show especially the chorionic appendage which projected as in Spec. A into the right cornu. Slightly reduced.
- Fig. 6. Fœtus, Spec. B, from the right side, after removal from the fœtal membranes. The severed umbilical cord is seen overlying the right fore-arm. Slightly reduced.
- Fig. 7. Chorionic appendage, Spec. B, extended so as to show the folded laminar character of the villi of its upper surface. Slightly reduced.
- Fig. 8. Portion of the same, more highly magnified.  $\times$  about 6.
- Fig. 9. Portion of the exposed surface of the chorionic appendage, Spec. B, showing the convoluted appearance of the villi.  $\times$  about 6.
- Fig. 10. Enlarged view of the portion of chorion, Spec. B, overlying left side of hinder region of fœtus, showing the folded villi and the non-villous ridged areas.  $\times$  about 6.
- Fig. 11. (Pl. VI). View of the inner surface of allanto-chorion after reflection of the inner wall of allantois (*all.w.*), showing the chorionic vesicles (*ch.ves.*).
- Fig. 12. Section through body of uterus, Spec. B.  $\times$  about 12.
- Fig. 13. Trans. section through the allanto-chorion in the region of junction of umbilical cord with the inner wall of allantois, showing the cord (*umb.c.*), the allantoic cavity (*all.cav.*) crossed by two septa (*sept.*), the allanto-chorion (*all.ch.*) with its villi and two chorionic vesicles (*ch.ves.*), in the left one of which the opening (*op.*) is visible.  $\times$  about 8.5.
- Fig. 14. Section similar to the preceding, more highly magnified to show the structure of the umbilical cord, allantois, and chorion.  $\times$  about 12.
- Fig. 15. Section through the allanto-chorion and one of its villi, showing the allantoic entoderm (*all.ent.*), the connective tissue of the allanto-chorion (*all.ch.*) prolonged to form the axis of the villus (*c.t.*), in which are seen in section the smaller branches of the allantoic vessels.  $\times$  about 48.
- Fig. 16. Section through a villous branch, to show the trophoblast (*tr.*), the underlying capillary plexus (*cap.*), and the connective-tissue core (*c.t.*). Note the characteristic zone of the latter, below the capillaries (*c.t'.*).  $\times$  about 360.

52. On the External Characters of the Beaver (*Castoridæ*)  
and of some Squirrels (*Sciuridæ*). By R. I. Pocock,  
F.R.S., F.Z.S.

[Received October 20, 1922 : Read November 21, 1922.]

(Text-figures 38-60.)

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*Introduction.*

The Squirrels, Marmots, and other admittedly related genera forming the *Sciuridæ* were formerly associated with the Beavers, or *Castoridæ*, in a primary division of the *Simplicidentate Rodents*, the *Sciuromorpha*\*. It has become the fashion in recent years to drop this group. Nevertheless, the two families are still suggestively juxtaposed by systematic writers, and no one seems to doubt the validity of the claim of their relationship based upon certain cranial characters connected more particularly with the structure of the zygomatic arch. Miller, for example, in his key to the families of Rodents of Western Europe, places the *Castoridæ* and *Sciuridæ* under a heading distinguished from the other families by having the anterior portion of the zygomatic arch formed chiefly by the jugal bone and the infraorbital foramen small; and the opening words of his diagnosis of the family *Castoridæ* are "characters essentially as in the *Sciuridæ*." Alston, Thomas, Flower, Tullberg, Winge, Max Weber, and others all agree in placing the *Castoridæ* and *Sciuridæ* in the same section of Rodents.

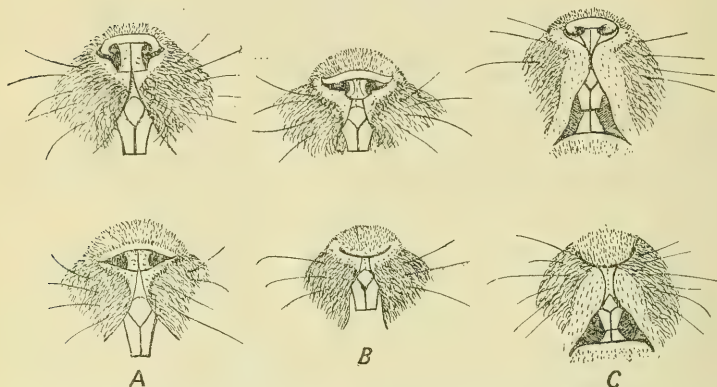
As regards the division of the *Sciuridæ* into subfamilies there has been, and is still, some difference of opinion. By most authors the Marmots and Sousliks were separated as a subfamily—*Arctomyinæ* (*Marmotinæ*)—from the Squirrels (*Sciurinæ*); but

\* Also containing the *Aplodontidæ*, about which I have no first-hand knowledge. This family was, however, removed from the *Sciuromorpha* by Thomas, P. Z. S. 1896, p. 1015.

Forsyth Major and Miller withheld that rank from them. On the other hand, the Flying Squirrels, which were usually distinguished as the subfamily *Pteromyiinae* (*Petauristinae*), were granted by Miller the full family rank as *Petauristidae*, equivalent to the rest of the Squirrels or *Sciuridae*. A fourth subfamily—*Nannosciurinae*—admitted as valid by some authors, was shown by Thomas in 1915\* to be composed of heterogeneous elements, the evidence of affinity between the genera derived from skulls being entirely untrustworthy.

The question of the generic classification of the *Sciuridae* need not be discussed at length. All that it is necessary to say is that in 1915 Thomas clearly showed, by his study of the *os penis*

Text-figure 38.



- A. Muzzle of *Sciurus vulgaris*, with rhinarium exposed and partially concealed by hood.  
 B. The same of *S. saltuensis*, with rhinarium exposed and entirely hooded.  
 C. Ditto of *Geosciurus capensis*.

or *baculum*, that previous attempts to affiliate the genera and subgenera by their skulls and teeth and other characters had in many instances yielded erroneous results, such as association of *Callosciurus* with *Sciurus* and of *Nannosciurus* with *Myosciurus*. No living student of the family would claim that we know the relationship of all the groups of genera to each other. The vagueness and diversity of opinions on this point, coupled with the hope of finding unrecorded features of systematic value, induced me to take up the study of the external characters presented by the ears, feet, and other organs which had been for

\* Ann. & Mag. Nat. Hist. (8) xv. p. 386.



the most part neglected by previous workers, partly owing to scarcity of materials, either fresh or preserved in alcohol, suitable for the purpose. The result of my observations, extending over many years and based upon specimens that died in the Zoological Gardens, form the subject-matter of the present paper. Examples of a good many genera have passed through my hands in that way; but in some cases I have been compelled to rely upon dried skins contained in the collections of the Zoological Society and of the Natural History Museum\*.

*The Muzzle, Mouth, and Facial Vibrissæ.*

The muzzle in all the genera of Sciuridæ and Petauristidæ is very uniform in structure. A peculiarity of the rhinarium is the mechanism by which the nostrils are closed. The hairy skin of the muzzle just behind it on the dorsal side is capable of being moved downwards and forwards, carrying the supranarial portion of the rhinarium with it, the two constituting, as it were, a kind of hood or cap over the nostrils. When completely lowered, the inferior edge of this hood forms a transverse or crescentically curved line defined from the upper lip by a narrow slit of the same shape. The line along which the upper half of the rhinarium is folded down is usually, at all events, marked by a transverse groove just above the upper edge of the nostrils. The rhinarium itself is naked and has a well-marked median groove between the nostrils, which are of the usual shape, with the typical narial slit behind and externally, and the expanded orifice in front and internally. They are moderately widely separated and look straight forwards. The rhinarium varies somewhat in shape. For instance, in *Sciurus vulgaris* it is comparatively deep, and has a nearly straight or convexly rounded upper edge. In *Sciurus saltuensis* it appears to be lower with the upper edge not nearly so raised. It also appears to be broader and altogether larger relatively in *Marmota* than in *Cynomys*. But although these observations were made upon fresh specimens, the apparent height of the rhinarium varies so much in accordance with the expansion or contraction of the hood, that I have found it impossible to make any useful systematic generalisations with regard to its shape. (Text-figs. 38 & 39, A-C.)

The two halves of the upper lip are completely divided up to the inferior median point of the rhinarium.

The rhinarium in *Castor* is very different from that of the Squirrels. The nostrils are widely separated, look outwards and upwards and are valvular, closing to form a crescentic slit. The area around them is naked, and the wide naked internarial space has an oblique crest of hairs passing over the nostrils on

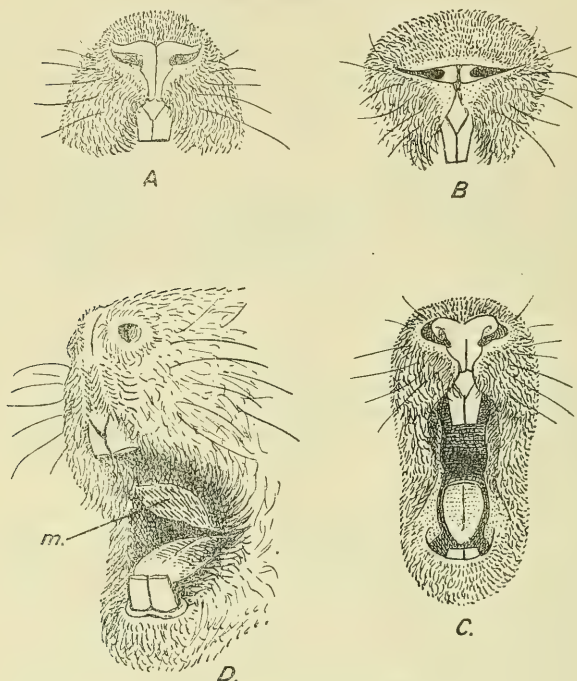
\* I have to thank Mr. Oldfield Thomas not only for permission to examine the collections under his charge, but also for much kind help in the identification of some of the species of this difficult group about which I was in doubt.



each side, and there is an upstanding crest on each side of the front of the infranarial portion of the rhinarium. The rhinarium is not mesially grooved and the upper lip is not cleft, although the short hairs on each side of the middle line are inclined inwards and downwards in a different direction from those external to them and form a definite crest or fringe. (Text-fig. 40, A, B.)

The *mouth* in Sciuridae and Petauristidae is provided with two palatal lobes of hairy integument jutting inwards from the

Text-figure 39.



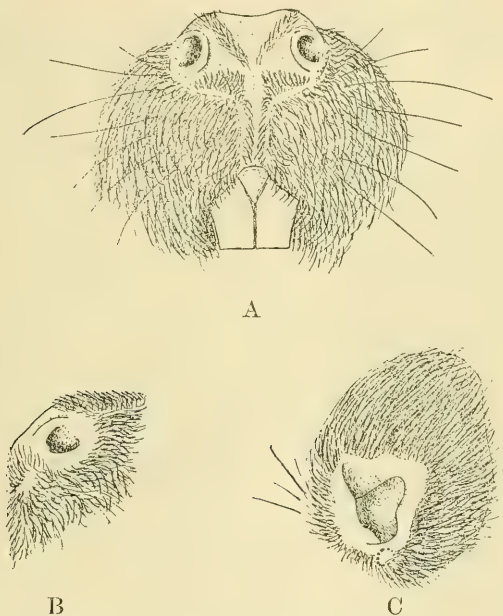
- A. Muzzle of *Cynomys ludovicianus*, with rhinarium exposed.
- B. " " *Ratufa indica*, with rhinarium partially hooded.
- C. Mouth and muzzle of *Marmota marmota*, showing the cheek-lobes projecting into mouth, and rhinarium exposed.
- D. Mouth and muzzle of *Castor canadensis*, half side view, to show mat of bristles (*m.*) inside the cheek.

cheek. These are capable of meeting over the palate behind the incisor teeth, but they are never fused in the middle line. Two similar but smooth and altogether smaller lingual lobes jut inwards on each side of the tongue. (Text-fig. 39, C.)

Definite cheek pouches are developed only in three genera—*Tamias* (*Eutamias*), *Citellus*, and *Cynomys*. I have not been able to examine them in *Citellus*, but in *Tamias* and *Cynomys* they

open into the mouth approximately on a level with the anterior end of the molar teeth. In *Tamias* they are of large size, and, when unstretched, reach back as far as the ear. In *Cynomys* they are much smaller and do not reach beyond the eye. Judging from the descriptions of the pouch of *Citellus* as "large," I presume it resembles that of *Tamias* and *Eutamias*. *Marmota* is usually described as being without cheek pouches, and I failed to find a trace of them in the typical European species *M. marmota*. Nevertheless, in his diagnosis of the genus, Miller

Text-figure 40.



- A. Muzzle and rhinarium of *Castor fiber*.  
 B. Rhinarium of the same from the side.  
 C. Ear of *Castor fiber*, with position of orifice dotted in.

says "cheek pouches rudimentary or absent." Elliot\* describes them as small in the American species, assigned to *Marmota*, and Cory† cites their presence as a character of the subfamily *Marmotinae*. (Text-fig. 41, C, D.) Fresh information is clearly wanted on this point.

In its palatal and lingual lobes the mouth of *Castor* resembles that of the *Sciuridae*, but it differs in having a large pad on each side of the cheek, lying farther within the mouth than the normal lobes. Each of these pads is provided with stiff, short

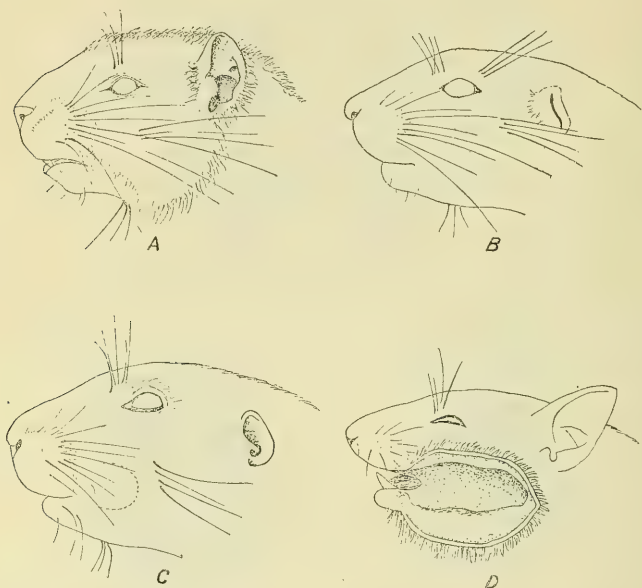
\* Field Columbian Museum, Zool. ii. p. 104, 1901.

† 'The Mammals of Illinois and Wisconsin,' p. 137, 1912.

hairs, forming a kind of mat, and projecting downwards and backwards. The hairs of these pads meet in the middle line over the tongue in front of the molar teeth, and close the orifice of the throat. (Text-fig. 39, D.)

The tufts of the facial vibrissæ in all the genera of true Squirrels, in the Sousliks and Marmots are normal in number and position, the mystacials, superciliaries, and genals being long and comparatively numerous and the interramals, though less evident, being always detectable. The only variations to record

Text-figure 41.



- A. Head of *Callosciurus prevosti*, showing the tufts of vibrissæ characteristic of the Sciuridæ.
- B. " " *Geosciurus capensis*, with additional tuft of superciliary vibrissæ.
- C. " " *Cynomys ludovicianus*, the curved dotted line showing the size and position of the small cheek-pouch.
- D. " " *Eutamias quadri vittatus*, with the external wall of the large cheek-pouch cut open.

are the absence of the interramal tuft in the Flying Squirrels (Petauristidæ) and the presence in the Bristly Ground Squirrels (*Xerus* and its allies) of a supplementary superciliary tuft of long vibrissæ over the posterior angle of the eye. In this particular these Ground Squirrels are unique, so far as I know, amongst mammals. (Text-fig. 41.)

The Beavers have a few short, stiff mystacial and superciliary vibrissæ, but the genal and interramal tufts are absent. In the

absence of the genal tufts the *Castoridæ* differ from the *Sciuridæ* and *Petauristidæ*.

The systematic results yielded by the characters discussed may be tabulated as follows:—

- a.* Rhinarium unhooded, not wholly naked, nostrils wide apart, lateral, valvular; upper lip uncleft; mouth with a bristly pad inside the cheek; no genal vibrissæ ..... *Castoridæ*.
- a'.* Rhinarium hooded, *i. e.* capable of being covered by a flap of skin from the upper surface of the nose, naked, nostrils close together, looking forwards, not valvular; upper lip deeply cleft to rhinarium; mouth without bristly pad inside cheek; genal vibrissæ present ..... *Sciuridæ* & *Petauristidæ*.
- b.* Two tufts of superciliary vibrissæ, an anterior and a posterior. *Xerus* and its allies.
- b'.* Only the normal anterior tuft of vibrissæ present.
- c.* Interramal tuft of vibrissæ present ..... *Sciuridæ* (including *Xerus*).
- c'* Interramal tuft of vibrissæ absent ..... *Petauristidæ*.

### *The Ear.*

In the arboreal Squirrels the ear exhibits no marked structural variations. That of *Sciurus vulgaris* may be described as typical. It is oval in shape and stands away from the head from a point in front about on a level with the supratragus, and behind from a point below the antitragus. The anterior edge is folded over from the summit or tip of the ear, and the overfolded rim increases in thickness down to the supratragus. Beneath the supratragus the edge runs obliquely downwards and backwards into the cavity of the ear, and ceases on its inner wall about midway between the supratragus and the orifice of the ear. The orifice lies at the bottom of the cavity just below the level of the intertragal notch, which is defined in front by a small hemispherical tragus and behind by a large angular antitragus. The latter fits over the tragus when the ear is closed, and posteriorly is continuous with a large flap resulting from the overfolding of the posterior rim from a point a little above the line of the supratragus. The supratragus is a ridge with sharply defined inferior and poorly defined superior edge. It forms the upper border of the cavity of the ear, separating it from the feebly hollowed upper portion, which in height exceeds the height of the cavity. (Text-fig. 42, A.)

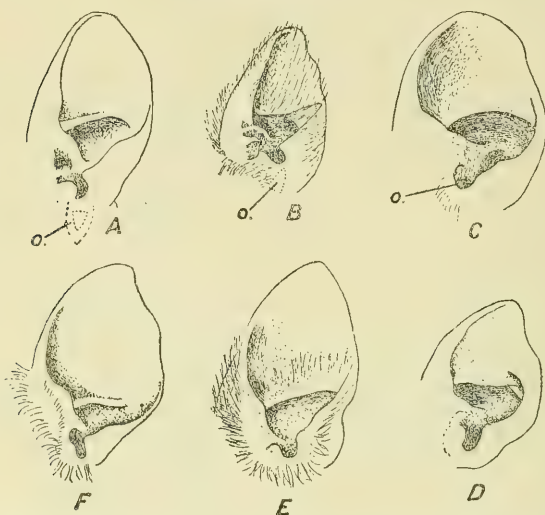
Judging from dried skins and material preserved in spirit, the ears of the American species *S. hudsonicus*, *carolinensis*, *niger* (*rufiventer*), *griseus*, *saltuensis*, *hypopyrrhus* and of several forms related to the last, resemble in all essentials those of *S. vulgaris*. So also do the ears of *Eutamias*, and of the *Petauristidæ* of the genera *Glaucomys*, *Eoglaucomys* and *Petaurista*, with the exception that in those Flying Squirrels the pinna is still more extended above the supratragus and the anterior edge is not overfolded to the summit. (Text-fig. 42, B, E, F.)

The ears of the Tropical Asiatic and African arboreal Squirrels differ from those of *Sciurus vulgaris* and of the American species above referred to in being shorter as compared with their antero-posterior width, in being less tubular at the base, so that the

auditory orifice opens approximately on a level with the intertragal notch; the tragus and antitragus, especially the latter, are, on the whole, less well developed, and the summit of the ear does not project so high above the level of the head, although in *Ratufa* and *Funambulus* it is in this respect intermediate between the ears of *Sciurus vulgaris* and its allies and those of *Callosciurus* and *Funisciurus*.

In *Ratufa* (text-fig. 42, C) the ear rises from the head at a point about on a level with the anterior end of the supratragus in front and below the upper end of the antitragal thickening behind; its upper edge is rounded, not pointed, and the edge of the anterior margin is overfolded from the summit. Inferiorly the over-

Text-figure 42.



A. Ear of *Sciurus vulgaris*.

D. Ear of *Funambulus palmarum*.

B. " " *Eutamias quadrivittatus*.

E. " " *Eoglaucomys fimbriatus*.

C. " " *Ratufa indica*.

F. " " *Glaucomys volans*.

o., position of orifice.

(These figures are intentionally drawn of approximately the same size.)

folded edge is continued downwards and backwards into the cavity of the ear, ceasing near its middle. Beneath its termination there is a shallow pit concealed within the antitragal thickening, which is low and not produced. There is no tragus, and the auditory orifice is just exposed within the intertragal notch. In *Callosciurus prevosti*, *C. notatus*, and *Tomeutes vittatus* the ear is less prominent than in *Ratufa*, and its points of attachment to the head in front and behind are somewhat higher. In *C. prevosti* also its upper portion is narrower and more pointed. In *C. vittatus* and *C. notatus* the posterior edge



is slightly emarginate above. In these three species the tragus is small or absent. (Text-fig. 43, A, B.) In *Funambulus tristriatus* the ear does not appear to differ in any essential points either in structure or relative size from that of *C. notatus*; but in *F. palmarum* it is less hairy and relatively considerably larger and has the posterior edge markedly emarginate above\*. (Text-fig. 42, D.)

In the African Squirrels, *Funisciurus leucostigma* and *F. cepapi*, the ears are small as in *Callosciurus*, and do not appear to differ from them, although the cavity is perhaps more subdivided by hollows and low ridges; but in *Heliosciurus punctatus* the anti-tragus is better developed, being provided with a very definite process; the tragus is a curved, soft ridge, and the orifice of the ear, normally concealed by the antitragus, is narrowed and pointed above instead of being subcircular as in *Funisciurus*. (Text-fig. 43, C, D.)

The ears of the *Citellus*, *Cynomys*, and *Marmota* are mostly smaller than in the typical Squirrels; but within the limits of the genus *Citellus* the variation in size is considerable. In *C. (Otospermophilus) beecheyi* they are indeed relatively larger than in *Callosciurus* or *Funisciurus* and project above the level of the head; but in other species, *i. e.* some of those referred to the subgenus *Ictidomys*, they have been described by Allen as "generally small, sometimes rudimentary." Nevertheless, even in *C. beecheyi* they differ structurally from the ears of all the typical Squirrels examined. The cavity of the ear, bounded above by the supratragus, is to a considerable extent filled in front by a thickened development of the inferior continuation of the overturned anterior margin of the pinna; and this thickening is covered closely with longish hair covering the cavity and closing it when the ear is folded. There is no trace of tragus or antitragus, the lower rim of the cavity forming an evenly curved line. For the rest, the area above the supratragus is well developed and has a very distinctly emarginate posterior border; the tip is somewhat pointed, and the overfolding of the edge of the anterior rim does not quite reach the summit. In front the ear rises from the head at a point a little above the anterior end of the supratragus, and behind the posterior border fuses with the integument of the head just below the posterior end of that ridge. (Text-fig. 44, D.)

In *Marmota marmota* the ear is a little more reduced in size than in *C. beecheyi*, and the area above the supratragus is wider in proportion to its height; the tip is pointed, but the posterior border is less markedly emarginate. The points of origin of the free portion in front and behind are approximately at the same

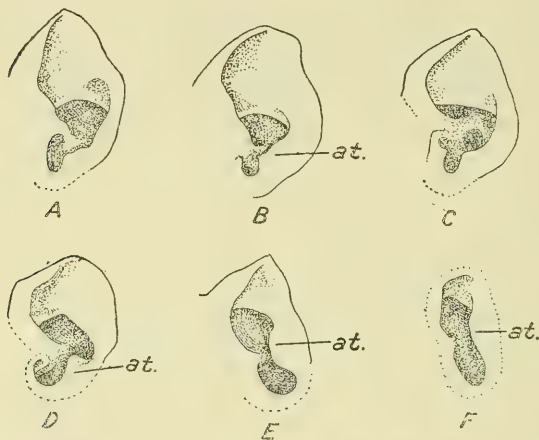
\* Judging from dried skins the ears of *Tomomys* seem to be like those of *Callosciurus*; but in the remarkable Bornean genus *Rheithrosciurus* these organs differ from those of the other Oriental genera in their great length. In this respect they surpass the ears of *S. vulgaris*; but details of their structure could not be determined on the made-up skins in the Natural History Museum.

levels as in *C. beecheyi*; the cavity is similarly blocked in front by the hairy thickening of the injutting portion of the inferior continuation of the overfolded portion of the anterior rim, and there is no trace of tragus, antitragus, or intertragal notch. (Text-fig. 44, E.)

In *Cynomys* the ear is very much smaller than in *Marmota* owing to the reduction in size of the area above the supratragus. The summit is rounded, and has its edge overfolded in continuation of the overfolding of the anterior edge. The hairy thickening projecting backwards into the cavity of the ear above the orifice is well developed, there is no tragus or intertragal notch, and at most a trace of antitragal thickening. (Text-fig. 44, F.)

In the Ground Squirrels of the genus *Xerus* and its allies, which are as terrestrial in their habits as the Sousliks and

Text-figure 43.



- |                                          |                                           |
|------------------------------------------|-------------------------------------------|
| A. Ear of <i>Callosciurus prevosti</i> . | D. Ear of <i>Heliosciurus punctatus</i> . |
| B. „ „ <i>Tomeutes vittatus</i> .        | E. „ „ <i>Atlantoxerus getulus</i> .      |
| C. „ „ <i>Funisciurus cepapi</i> .       | F. „ „ <i>Geosciurus capensis</i> .       |

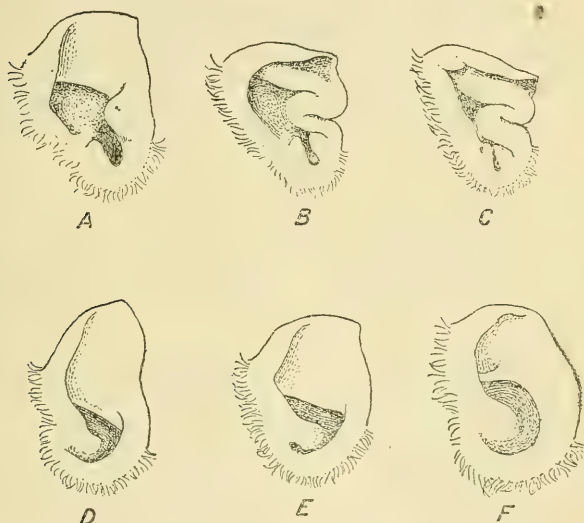
at., antitragal thickening.

Marmots, the ears are greatly reduced in size, in some cases, indeed, *e.g.* in *Geosciurus capensis*, equalling apparently in that respect those of some of the small-eared species of *Citellus*. But they are modified for terrestrial life on quite a different plan from that exhibited by the Sousliks and Marmots.

In *Euxerus erythropus*, for instance, a comparatively large-eared form, in which the summit of the ear reaches about as high as the level of the head, the antero-superior and posterior margins meet approximately at a right angle. The anterior edge is overfolded, and is continued beneath the supratragus, where it bends backwards and downwards, ceasing just above the tragus, or sometimes running thence backwards and upwards as

a rod-like ridge to the posterior end of the supratragus. The tragus is a hard, rounded eminence, and the intertragal notch is very deep. The antitragus is a thick bulging swelling set high above the tragus just beneath the posterior end of the supratragus, which fuses with it. The anterior edge rises from the head at a point about on a level with the anterior end of the supratragus and the posterior edge, which is nearly straight or slightly sinuous, from a point about on a level with the lower portion of the antitragal prominence. When the ear is closed the upper portion folds down on the supratragus, the antitragus is folded on itself and pulled forwards over the tragus, and with the supratragus blocks the upper part of the cavity, the intertragal notch at the same time being closed by the juxtaposition

Text-figure 44.



- A, B, C. Ear of *Euxerus erythropus*, in three stages of folding.  
 D. Ear of *Citellus (Otospermophilus) beecheyi*, from a dried skin.  
 E. " " *Marmota marmota*.  
 F. " " *Cynomys ludovicianus*.

of its anterior and posterior walls. Thus the mechanism for closing the ear is quite different from that of the Marmots and Sousliks, where the supratragus is depressed against the hairy thickening invading the fore part of the ear-cavity, the thickening itself being pressed down over the orifice. Judging from a dried skin, the ear of *Xerus rutilus* is relatively a little smaller than in *Euxerus erythropus* owing to the reduction in size of the portion above the supratragus. (Text fig. 44, A-C.)

In *Atlantoxerus getulus* the ear seems to be relatively a little smaller than in *E. erythropus*, and projects from the head less

prominently, but resembles it in other ways sufficiently closely to call for no detailed description. The most important difference is the absence of the tragal thickening in front of the intertragal notch, so that the orifice of the ear is exposed. Owing to the reduction in size of the upper free portion, the supratragus is nearer to the summit and the latter is somewhat more pointed. (Text-fig. 43, E.)

The ear of *Geosciurus capensis* exhibits the final stage in degeneration in this group\*; but it is clearly derivable from the type seen in *Atlantoxerus* by the reduction of the upper portion above the supratragus to a rounded thickened rim incapable of being folded downwards and backwards to any appreciable extent on to the supratragus, which is represented at most by a short ridge running forwards and upwards from the antitragus. The latter, as in the other species, is a rounded thickened bulge, less well defined than in the northern species, set high up and overlapping the posterior portion of the cavity. The anterior rim is overfolded, and its inferior continuation into the cavity is represented at most by a small excrescence opposite the antitragus. There is no tragus, as in *Atlantoxerus*, the orifice being exposed at the bottom of the deep intertragal notch. The ear is closed by the forward movement of the thicker posterior border of the cavity against the anterior, there being no folding of the antitragus or upper rim. (Text-fig. 43, F.)

The structure of the ears in these Bristly Ground Squirrels is not opposed to the view of their affinity with the African species referred to *Funisciurus*, but the differences supply no evidence of close affinity.

In *Castor* the ear is relatively small, but is as free from the integument of the head as in the typical Sciuridæ. Its outer surface is flat, and the anterior edge is not overfolded; it is uniformly covered with hair except round the cavity, where it is naked. The cavity is a small, irregularly triangular space bounded above by the supratragus, which is overlapped in front by the anterior edge which runs downwards and backwards to the orifice lying at the bottom of the cavity and concealed by the lower edge of the cavity corresponding to the intertragal notch. The posterior border of the cavity forms a convex bulge probably representing the antitragus, but there is no trace of tragus. (Text-fig. 40, C.)

The characters of the principal types of ears above described may be summarised as follows:—

- |                                                                                                                                                                       |                                    |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------|
| a. Ear simple, its anterior edge above the supratragus not overfolded .....                                                                                           | <i>Castor.</i>                     |
| a'. Ear simple or complex, its anterior edge above the supratragus overfolded.                                                                                        |                                    |
| b. Cavity of the ear, when folded, mainly closed by hairy, thickened continuation of the overturned anterior rim beneath the supratragus, no tragus or antitragus ... | <i>Citellus, Cynomys, Marmota.</i> |

\* Described by W. L. Schlater as follows:—Ear conch completely absent, the ear-opening being a narrow diagonal slit half an inch in length.



- b'. Cavity of the ear, when folded, mainly closed by antitragus, the inferior continuation of the overfolded anterior border not forming a hairy thickening within the cavity.
- c. Antitragal thickening set high up near the middle of the posterior wall of the cavity; pinna reduced.
- d. Margin of ear a thickened rim not standing away from the head .....
- d'. Margin of ear standing away from head dorsally ... *Geosciurus*, *Xerus*, *Euxerus*, *Atlantoxerus*.
- e'. Antitragal thickening occupying normal position and forming the postero-inferior wall of the cavity; pinna standing well away from head dorsally ..... Typical Squirrels, *Tamias*, *Petauristidæ*.

Although *Castor* is isolated at the head of this table, it can hardly be claimed that its ears differ more from those of typical Squirrels than do the ears of *Geosciurus*. Section c' is roughly divisible into two groups, exemplified respectively by *Sciurus* and its near allies, *Tamias* and the *Petauristidæ*, which have long or comparatively long ears, and by the tropical African and Asiatic genera *Funisciurus*, *Heliosciurus*, *Callosciurus*, and *Ratufa*, where the ears are shorter and less tubular at the base. But these groups seem to intergrade. What the ears of *Rheithrosciurus* are like apart from length has yet to be ascertained.

#### The Feet.

The feet of the typical arboreal Squirrels of the family Sciuridæ have many characters in common. In the fore foot the first digit is reduced to an apparently functionless excrescence springing from or imbedded in the side of the inner carpal pad, and carrying a nail. Of the remaining digits, the fourth is the longest, the difference between the fourth and the fifth or second being considerable. The fourth and the third are more closely united at the base than they are to the fifth or second respectively, and the middle line of the artiodactyle foot passes between them. The digital pads and claws are well developed. The plantar pad is always represented by three well-defined elements. The undersides of the digits and of the sole are typically naked—hairy in some northern forms in winter,—and there are two well-developed carpal pads, of which the inner is the larger of the two. The tuft of carpal vibrissæ is always present and large.

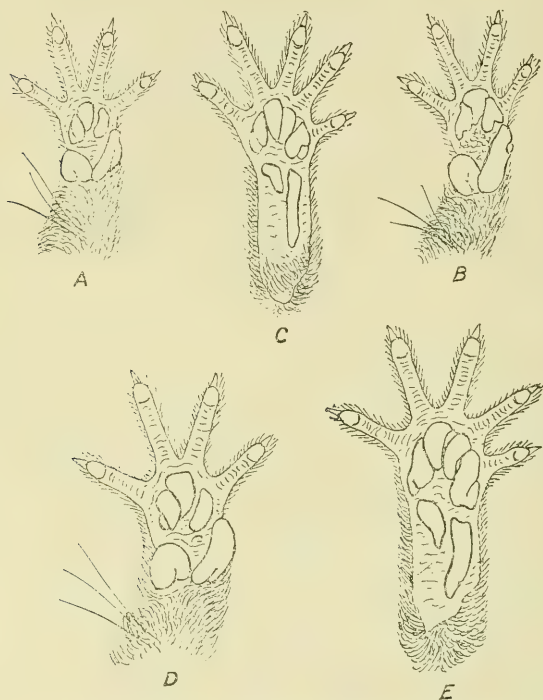
The digits of the hind foot resemble those of the fore foot tolerably closely in structure and relative lengths, the fourth being the longest; but the first digit is well developed and resembles the others, except that it is much the shortest of the series. The well-developed plantar pad consists of four lobes. The metatarsal area is for the most part naked, the heel alone generally being hairy, and is supplied with two pads, an inner, which is the larger, and an outer, which, in addition to being smaller, is set more forwards. Sometimes one or both of these pads is suppressed, in the case, for instance, of Squirrels, which have hairy feet in the winter, e. g. *S. vulgaris*.



a. Feet of the Tropical Asiatic Squirrels.

In *Callosciurus prevosti* the claws of the fore foot are short, with an abruptly curved, sharp point; the three main elements of the plantar pad are large and elongated, and small accessory tubercular pads are sometimes associated with them. The outer carpal pad is irregularly cordate, with a notch in its posterior border; it is much shorter than the inner carpal pad,

Text-figure 45.



- A. Right fore foot of *Callosciurus notatus*, nat. size.  
 B. " " " " *Tomeutes vittatus*.  
 C. " hind " " " "  
 D. " fore " " *Callosciurus prevosti*.  
 E. " hind " " " "

which extends forwards along the side of the foot, so that its anterior end overlaps on the pollical side the posterior end of the internal lobe of the plantar pad, and its pollical margin, evenly convex, conceals from view from the lower side the nail of the pollex, which is planted some distance behind the anterior end of the pad. (Text-fig. 45, D.)

The hind foot has claws like those of the fore foot, and the four lobes of the plantar pad are similarly large and long, especially the internal; and both the internal and the external lobes are provided with a small supplementary lobe, making the entire plantar pad appear to be composed of six lobes, four large and two small. The metatarsal pads are also large. The internal starting close behind the corresponding lobe of the plantar pad and extending backwards to within a short distance of the hairy heel, occupies about one-third of the naked metatarsal area. The external metatarsal pad, about equal in area to the median lobe of the plantar pad, extends obliquely inwards and backwards from a point close behind the plantar pad, its posterior end overlapping the anterior end of the internal metatarsal pad. (Text-fig. 45, E.)

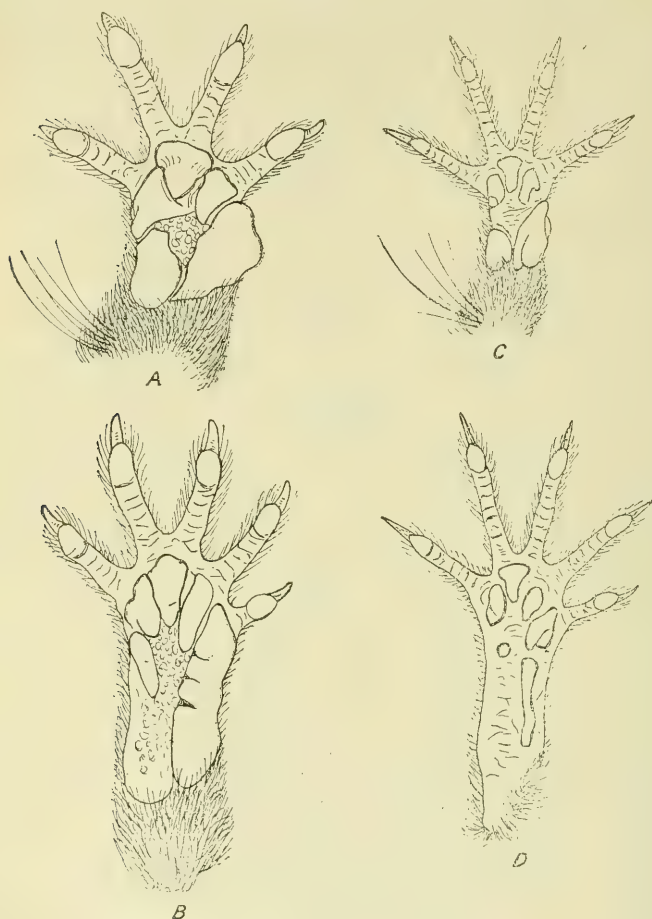
The feet of *Callosciurus notatus* and of *Tomeutes vittatus* are practically alike and agree in all essential respects with those of *C. prevosti*, and judging from dried skins *Callosciurus finlaysoni*, *C. castaneiventris*, and *Tomeutes hippurus* have feet of essentially the same type. (Text-fig. 45, A, B, C.)

In *Ratufa indica* the fore foot has the pads exceedingly large. The three plantar pads are in contact with each other and with the two carpal pads. The latter meet posteriorly, and the five pads form a continuous lobate cushion surrounding a depressed area of soft but coarsely granular integument. The inner carpal, with which the digital pad of the pollex is indistinguishably fused, is as large as the three lobes of the plantar pad taken together. It forms a large projection on the inner side of the foot behind the second digit, and constitutes a grasping organ with the tips of the four digits, which close obliquely upon it. (Text-fig. 46, A.) In the hind foot development of the pads reaches its maximum, as is the case in the fore foot. The four lobes of the plantar pad are wide, long, and in contact, and form a continuous cushion, with undulating distal margin extending from the inner to the outer edge of the foot. The outer metatarsal pad, moreover, is elongated and in contact at its distal end with the outer lobe of the plantar pad; and the inner metatarsal pad is similarly confluent with the inner lobe of the plantar pad, the two together forming a long cushion about half the width of the metatarsal area, and reaching back to the hairy heel. The soft integument of the sole surrounded by the plantar and metatarsal pads and the outer half of the sole as far back as the proximal end of the inner metatarsal pad is granular, the granules being coarser distally behind the plantar pad than proximally towards the heel, which is covered with hair up to the proximal end of the inner metatarsal pad. (Text-fig. 46, B.)

*R. bicolor* and *R. macrourus* have feet like those of *R. indica*, and the claws of the genus *Ratufa* are short, abruptly curved, and sharply pointed like those of *Callosciurus*. The feet of *Ratufa*, indeed, may almost be described as an exaggeration of the type seen in *Callosciurus* by the expansion and fusion of the pads.

The feet of the Palm Squirrels (*Funambulus*) are relatively longer and thinner than those of *Ratufa* and *Callosciurus*, and have the pads less well developed. Otherwise they are tolerably

Text-figure 46.

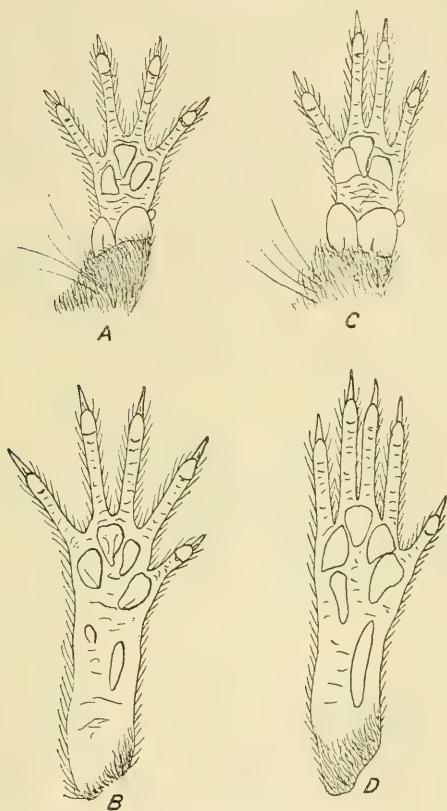


- A. Right fore foot of *Ratufa indica*.  $\times \frac{1}{3}$ .  
 B. " hind " " " "  
 C. " fore " " *Funambulus palmarum*, much enlarged.  
 D. " hind " " " "

similar to those of *Callosciurus*, the inner, or pollical, carpal pad being similarly elongated, so that its distal extremity considerably overlaps the inner lobe of the plantar pad. In the hind

foot the external and internal lobes of the plantar pad are often subdivided, but not always, and never to the same extent as in *Callosciurus*; the inner metatarsal pad is always long and rod-like, but the outer in all the specimens examined is small, spherical, and approximately on a level with the

Text-figure 47.



- A. Right fore foot of *Rheithrosciurus macrotis*.  
 B. " hind " " " "  
 C. " fore " " *Protoxerus stangeri*.  
 D. " hind " " " "

(These figures drawn without measurements from dried skins.)

distal end of the inner without overlapping it proximally. The heel is less hairy than in *Callosciurus* and *Ratufa*, being sometimes naked in the middle line, sometimes scantily hairy. (Text-fig. 46, C, D.)

Judging from dried skins\*, the feet of *Rheithrosciurus* are relatively longer and thinner than those of *Callosciurus*, and the claws are longer. In the fore foot the three plantar lobes are large, the median being well defined from the laterals. Of the carpal pads, the outer is the smaller and narrow, and the inner has an evenly convex margin and is not elongated and produced distally so as to overlap the plantar lobe of the same side. In the hind foot the four lobes of the plantar pad are not so large or so closely packed as in *Callosciurus*, and the outer and inner are at most indistinctly subdivided; the metatarsal area is naked to the heel, the outer metatarsal is considerably shorter than in other Oriental genera examined, and the inner metatarsal is small and subspherical as in *Funambulus* and many other genera of Squirrels. (Text-fig. 47, A, B.)

In the structure of the feet *Rheithrosciurus* is perhaps more like some of the American subgenera of *Sciurus* than it is like other Oriental genera.

The distinguishing characters of the feet of the Oriental Squirrels above described may be tabulated as follows:—

- |                                                                                                                                                                               |                                |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------|
| a. Pads enormous, internal carpal very prominent on the pollical side; metatarsal pads confluent with plantar pad, the internal nearly half the width of the metatarsus ..... | <i>Ratufa.</i>                 |
| a'. Pads less developed, internal carpal less or not noticeably prominent on pollical side; metatarsals not confluent with plantar pad.                                       |                                |
| b. Internal carpal long, narrowed distally, and overlapping plantar pad on inner side; internal metatarsal long.                                                              |                                |
| c. Feet shorter and stouter, plantar pad of hind foot larger, six-lobed, metatarsals thicker, external produced proximally beyond distal end of internal.                     | <i>Callosciurus, Tomeutes.</i> |
| c'. Feet longer and thinner, pads smaller; external metatarsal spherical set beyond distal end of narrowed internal metatarsal.....                                           | <i>Funambulus.</i>             |
| b' Internal carpal pad apically rounded, only a little longer than external and not reaching plantar pad; internal metatarsal relatively short.....                           | <i>Rheithrosciurus.</i>        |

#### b. Feet of the Tropical African Squirrels.

The two African species, *Funisciurus leucostigma* and *F. cepapi*, have feet of a more generalised type than those of the Oriental species of *Ratufa* and *Callosciurus* examined, the plantar, carpal, and metatarsal pads being less well developed. The plantar pad of the fore foot is three-lobed, of the hind foot four-lobed. The inner carpal pad is not so elongated distally, and the outer metatarsal is comparatively small, subcircular, or elliptical, and is set on a level with the anterior end of the long rod-like inner metatarsal or a little in front of it. Except that the feet are of stouter build, they differ but little from those of *Funambulus palmarum*, although in the latter the inner carpal pad is produced distally nearly as much as in *Callosciurus*. (Text-fig. 48, C-F.)

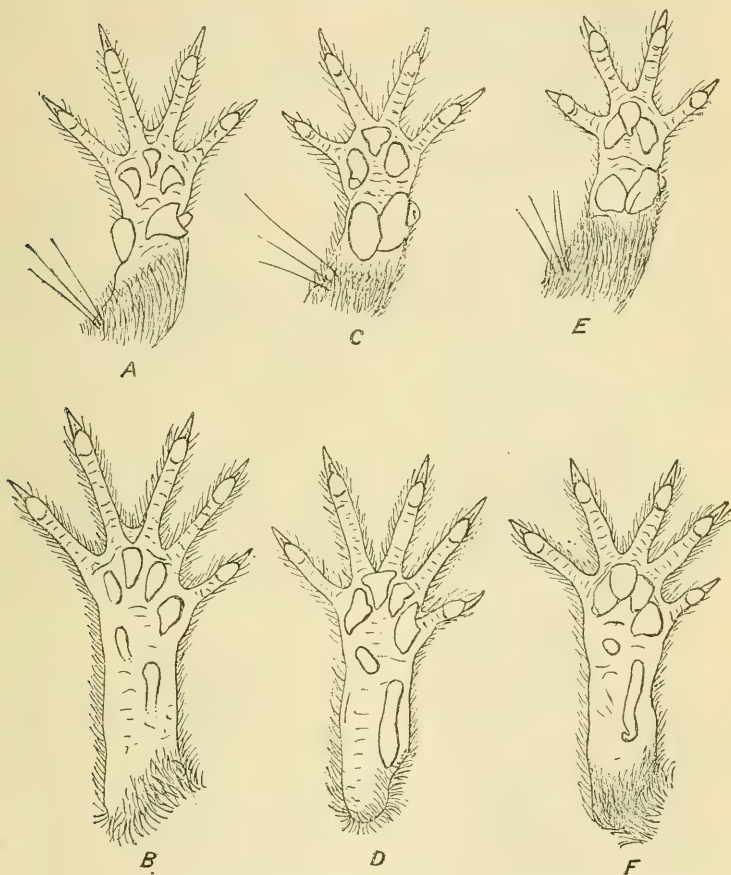
\* It must be remembered, however, that the proportions of the feet vary with the preservation. In fresh specimens they appear to be plumper and shorter than those contracted by alcohol, and the latter are, as a rule, less shrunk than the feet on dried skins.



Judging from dried skins, the feet of *F. isabella*, the type of the genus *Funisciurus*, resemble those of *F. leucostigma* and *cepapi*.

*Protoxerus stangeri* also has feet differing in no important

Text-figure 48.



- A. Right fore foot of *Heliosciurus punctatus*, nat. size.  
 B. " hind " " " " " "  
 C. " fore " " *Funisciurus cepapi*, " "  
 D. " hind " " " " "  
 E. " fore " " *Funisciurus leucostigma*, " "  
 F. " hind " " " " "

point from those of *Funisciurus*, although the outer metatarsal pad is much longer, being at least half as long as the inner. (Text-fig. 47, C, D.)

In *Heliosciurus punctatus* the feet are relatively larger than in *Funisciurus leucostigma*, the plantar lobes and carpal pads of the fore foot are smaller, more angular, and separated; in the hind foot the plantar lobes are also smaller and more spaced, the inner metatarsal is much shorter, being oval and well-defined distally but abbreviated and ill-defined proximally; the inner metatarsal is like it but smaller\*. (Text-fig. 48, A, B.)

The species belonging to the three African genera above discussed may be distinguished as follows by their feet:—

- a. Inner metatarsal pad very short, lobes of plantar pads and carpal pads relatively small and separated ..... *H. punctatus*.
- a'. Inner metatarsal pad a long, stout ridge; lobes of plantar pads and carpal pads larger and closer together.
- a<sup>2</sup>. Outer metatarsal pad elongate, more than half the length of the inner ..... *P. stangeri*.
- b<sup>2</sup>. Outer metatarsal pad small, oval or spherical ..... *F. leucostigma, cepapi*.

In a general sense the hind feet of *Funisciurus* do not differ in any very important respect from those of *Funambulus*; but all the African species examined differ from all the Oriental species in not having the same elongation of the inner carpal pad. In the length of the outer metatarsal *P. stangeri* approaches *Ratufa* and *Callosciurus*.

*Funisciurus leucostigma* and *cepapi*, on the one hand, and *Protoxerus stangeri*, on the other, were regarded by Forsyth Major as representing respectively two subgenera of *Xerus*. By their feet, however, they are typical arboreal Squirrels, differing in no essential particulars, so far as those organs are concerned, from such tropical American species as *Sciurus (Echinosciurus) hypopyrrhus*.

### c. Feet of the European and American Squirrels.

In the tropical American Squirrels, referred to a large number of subgenera of *Sciurus*, the soles of the feet are naked as in the tropical Asiatic and African forms, the heel being generally hairy although sometimes naked down the middle line, as in an example of *Sciurus saltuensis bondæ* that died early in October. The lobes of the plantar pads are well developed, the two carpal pads are subequal in size, the inner not projecting appreciably beyond the outer as it does in the tropical Asiatic forms. The two metatarsal pads are retained, the inner being thick, elongated, and curved, the outer smaller, ovate, and situated in front of the anterior end of the inner. The claws are longer than in the tropical African and Asiatic forms. The feet of *S. (Echinosciurus) hypopyrrhus* resemble those described above, and their soles are naked in mid-winter. (Text-fig. 49, D.)

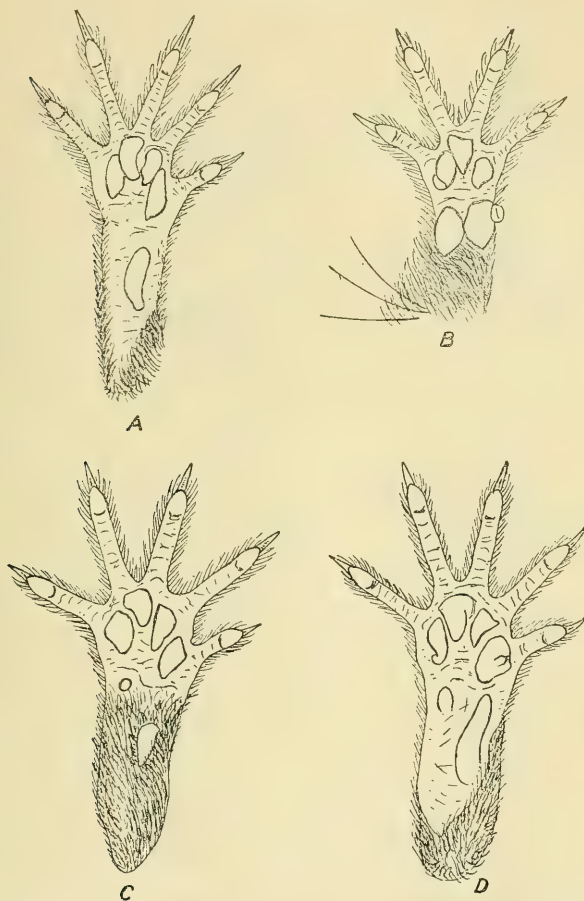
The feet of the Squirrels of the northern parts of America are, generally speaking, similar to those of the warmer latitudes, with this difference, that the soles undergo a seasonal change in the

\* For a tabulation of the genera of African Sciuridæ, based mainly on skulls and teeth, see Thomas's paper (Ann. & Mag. Nat. Hist. (8) iii. pp. 467-475, 1909).

matter of hair growth, accompanied in some cases by the suppression of one or both of the metatarsal pads.

In the North American Grey Squirrel (*S. (Neosciurus) carolinensis*) the outer metatarsal pad is sometimes absent. When

Text-figure 49.

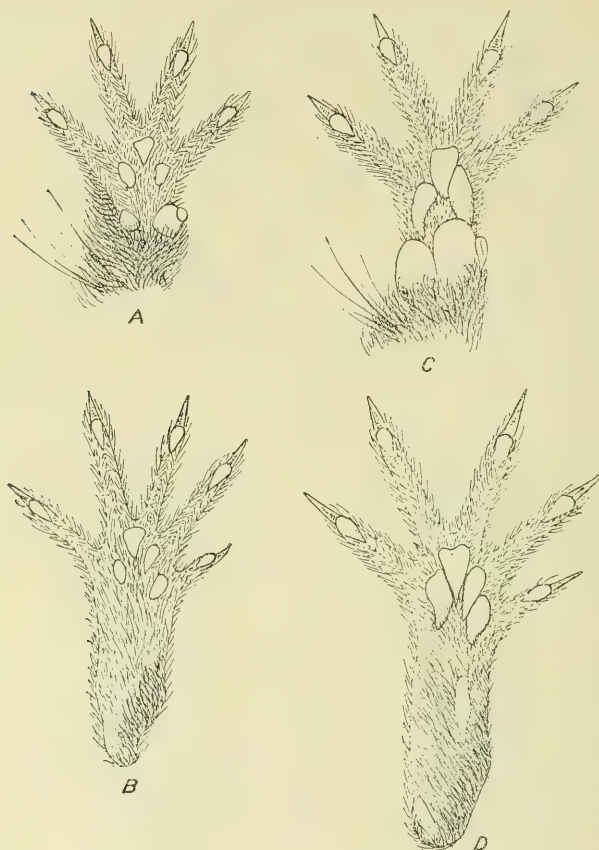


- A. Right hind foot of *Sciurus carolinensis*, with external metatarsal pad absent, in summer pelage (from dried skin).
- B. Right fore foot of the same, in winter pelage.
- C. „ hind foot of the same, in winter pelage, the external metatarsal retained.
- D. Right hind foot of *S. hypopyrrhus*, or closely related species, in mid-winter pelage.

retained it is a hemispherical tubercle set far forwards in front of the inner, which is irregularly ovate and shorter than in

the tropical species. An example examined in September had the sole of the hind foot naked except the heel, which was hairy, whereas one that died in the middle of December had the sole covered with hair as far down as the outer metatarsal pad.

Text-figure 50.



- A. Right fore foot of *Sciurus vulgaris*, mid-winter.  
 B. " hind " " " " " "  
 C. " fore " " *S. niger rufiventer*, " "  
 D. " hind " " " " "

(C, D from dried skin.)

The fore foot in the two specimens was quite naked beneath at both dates. Again, in a skin of a specimen of the North American Fox Squirrel *S. (Parasciurus) niger rufiventer*, which died at the beginning of December, all trace of the outer meta-

tarsal pad has disappeared, although the inner is somewhat larger and more elongated than in *S. carolinensis*, and the whole of the under side of the foot, including the digits, is covered thickly with hair, apart from this pad, the well-developed four-lobed plantar pad, and the digital pads. The latter are pointed at their proximal ends. The fore foot is similarly hairy, there being a distinct patch on the median area in front of the carpal pads and defined by the three elongated contiguous lobes of the plantar pad. I am not aware whether the soles of the feet in this species are naked in the summer or not; but analogy justifies the belief in this being so. (Text-figs. 49, A-C; 50, C, D.)

In *Sciurus vulgaris*\* and its subspecies the lower sides of the feet in summer are as naked as in tropical species, except that perhaps a larger area of the heel is hairy. The inner metatarsal pad is comparatively short and set some distance behind the plantar pad; the outer is quite small and some distance in front of the anterior end of the inner. But in winter the soles and lower sides of the digits are overgrown with hair which is more abundant on the hind than the front foot. In the hind foot it obliterates the metatarsal pads and passes between the lobes of the plantar pads. In both feet at this season the digital pads are reduced to long, narrow, posteriorly-pointed lobes. (Text-fig. 50, A, B.)

In the North American Red Squirrel, *S. (Tamiasciurus) hudsonicus*, I can find no trace of either of the metatarsal pads. According to C. B. Cory† the soles of the feet are "furred in the winter." From this statement I should infer that they are naked in the summer, were it not that a skin in the Zoological Society's collection in summer pelage, with untufted ears and black lateral stripe, has the metatarsus covered with hair almost down to the plantar pads, whereas the area round the plantar pads and the under sides of the digits are naked. The fore foot also is as naked as in tropical species of Squirrels. On the other hand, in the skin of a specimen that died on January 7th in winter pelage, with tufted ears and no lateral stripe, both fore and hind feet are covered with hairs beneath, as in the specimen of the Fox Squirrel described, only the digital, plantar, and carpal pads being naked. But whether the whole of the metatarsal area in the American Red Squirrel is mesially naked back to the heel in summer as in the European Squirrel, *S. vulgaris*, I do not know. (Text-fig. 51, A, B.)

#### d. Feet of the Chipping Squirrels (*Tamias*).

The feet of the Chipmunk, *Eutamias quadrivittatus*, do not differ materially from those of the typical Squirrels, except that the third and fourth digits are very nearly equal, the fourth at

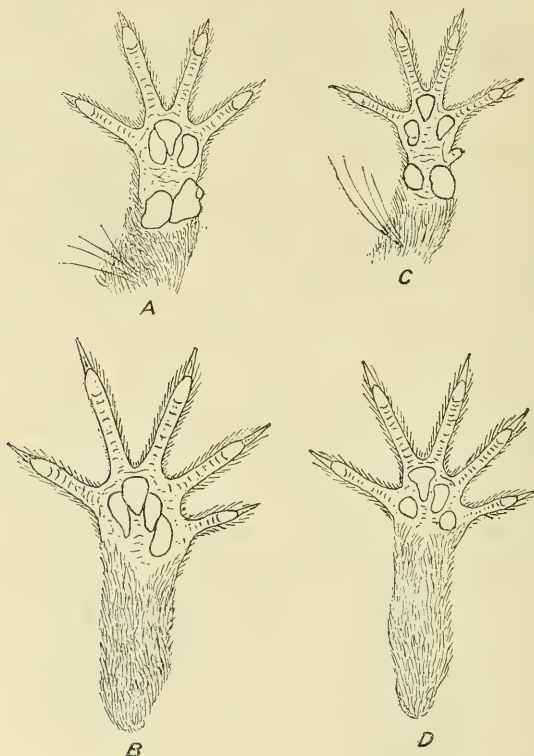
\* The feet, in summer and winter pelage, of the British representative (*S. leucourus*) of the species are figured and described by Barrett-Hamilton and Hinton ('A History of British Mammals,' pt. xxi. p. 699, pl. xxxvii.).

† 'The Mammals of Illinois and Wisconsin,' 1912, p. 123.



most exceeding the third very slightly. Nevertheless, the tip of the fourth extends beyond that of the second both in the fore and the hind foot. The feet are narrow and long, and the lobes of the plantar pads are not in contact, though well developed. The inner lobe of the carpal pad has a rounded distal border

Text-figure 51.



- A. Right fore foot of *S. hudsonicus*, in summer pelage (from dried skin).  
 B. " hind " " " same specimen.  
 C. " fore " " *Eutamias quadrivittatus*.  
 D. " hind " " " "

(A, B a little enlarged; C, D much enlarged.)

and is not produced beyond the margin of the smaller outer pad, and the small pollex projects a little in front of it, which is not the case in the typical Squirrels, where the pollex rises from the outer surface of the inner carpal. The under sides of the digits and the area round the plantar lobes are naked in both fore and hind foot; but in the hind foot the whole of the meta-

tarsal area is covered with hair down to the plantar pad, and there is no trace of metatarsal pads as in *S. (Tamiasciurus) hudsonicus*. (Text-fig. 51, C, D.)

This description of the feet of *Eutamias*, based upon a single individual, must not be taken as applying to all the species of *Tamias*. In some dried skins of this genus in the Natural History Museum, the digits appear to resemble those of *Citellus* rather than of *Sciurus* and its allies in relative lengths; and the metatarsal area is not so extensively haired as in the specimen of *Eutamias* described.

*e. Feet of the Bristly Ground Squirrels (Xerus, etc.).*

The feet of the African Ground Squirrels, *Atlantoxerus getulus*, *Xerus rutilus*, *Euxerus erythropus*, and *Geosciurus capensis* differ from those of the arboreal species hitherto described in having the third digit the longest and the fourth only a little longer than the second, so that the feet approach the perissodactyle type; the pollex is not suppressed to quite the same extent, but stands away as a distinct excrescence from the antero-external edge of the adjoining inner carpal pad, and this is not appreciably produced distally beyond the outer carpal; the metatarsal area is naked to the heel, and its pads are either absent or poorly developed.

In *Atlantoxerus getulus* the feet are long and slender and the digits more nearly approach those of the arboreal Squirrels in length, the third only slightly exceeding the fourth, which, in the fore foot, is decidedly longer than the second. The lobes of the plantar pads are large, well developed, the hallucal lobe on the hind foot being nearly as large as the others individually; the carpal pads also are comparatively large, and the metatarsal pads are at all events sometimes distinguishable, although small and oval. (Text-fig. 52, A, B.)

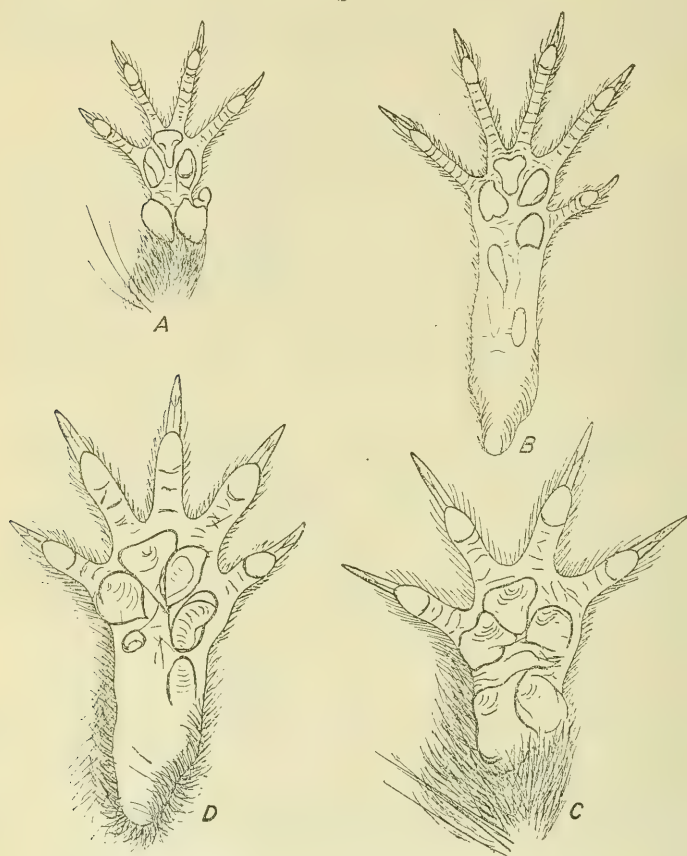
In *Euxerus erythropus* the fore foot is broader and shorter, with respect both to the digits and sole, than in *Atlantoxerus*; the plantar and carpal pads are relatively smaller and the claws are longer. The pollex is small but subcylindrical with a small pad remote from the carpal. In the hind foot, too, the claws are longer than in *Atlantoxerus*, the lobes of the plantar pad are considerably smaller, especially the outer and inner, the latter being a small subcircular tubercle at the base of the hallux, only about one-fourth the size of the median lobe; and there is no trace of metatarsal pads\*. (Text-fig. 53, A, B.)

In *Geosciurus capensis* the feet are more robust and more fossorial in character than in *E. erythropus*. In the fore foot the three lobes of the plantar pad are well developed but shorter

\* *X. rutilus* is known to me only from a dried skin. On this the plantar lobes appear to be somewhat larger relatively than in *E. erythropus*; but there is no trace of metatarsal pads, and the hallucal lobe of the plantar pad is small and isolated.

than in *Atlantoxerus* and in contact, and the pad of the pollex projects as a large lobe jutting out from the side of the adjoining carpal pad. In the hind foot the three main lobes of the plantar pad are also well developed, larger than in *Euxerus erythropus* but shorter than in *Atlantoxerus getulus*; but

Text-figure 52.



- A. Right fore foot of *Atlantoxerus getulus*, much enlarged.  
 B. " hind " " same.  
 C. " fore " " *Marmota marmota*.  $\times \frac{1}{3}$ .  
 D. " hind " " same.

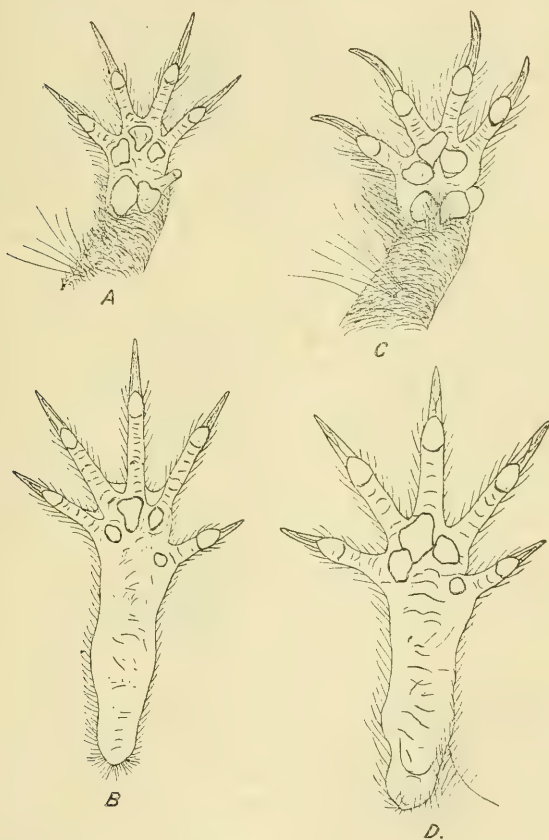
the hallucal lobe is quite small, subcircular and isolated as in *Euxerus erythropus*; and as in the latter there is no trace of metatarsal pads, and the claws of all the digits are long and strong.

The feet of the Xerine Squirrels above described differ as follows:—

- a.* Feet thinner; inner lobe of plantar pad of hind foot large, the metatarsal pads retained but poorly defined..... *Atlantoxerus.*  
*a'.* Feet stouter; inner lobe of plantar pad of hind foot very small, metatarsal pads absent.  
*b.* Plantar pads smaller, pollex a relatively small subcylindrical excrescence ..... *Euxerus.*  
*b'.* Plantar pads larger, pollex a conspicuous subcircular excrescence ..... *Geosciurus.*

The feet of *Xerus*, typified by *utilus*, fall under heading *a'* of this table.

Text-figure 53.



A. Right fore foot of *Euxerus erythropus*.  $\times \frac{1}{4}$ .

B. " hind " " " "

C. " fore " " *Geosciurus capensis*.

D. " hind " " " "

*f. Feet of the Sousliks and Marmots.*

A second group of Ground Squirrels represented by the Sousliks (*Citellus*) and the Marmots (*Cynomys*, *Marmota*) have feet like those of *Xerus* and its allies in that the third digit is the longest, and the second and fourth digits not so unequal, as in the arboreal Squirrels, and the claws longer, stouter, and less curved. The three genera in question, however, have very different feet.

The fore foot of *Citellus* (*Otospermophilus*) *beecheyi*\*, judging from a dried skin, is shorter and broader than that of the typical squirrels, and is naked below. The fourth digit is decidedly but not much longer than the second. The three lobes of the plantar pad and the two carpal pads are well developed, and the pollex is represented by a conspicuous nail attached to the outer side of the inner carpal pad in front. In the hind foot the second, third, and fourth digits are nearly equal, the third only slightly surpassing the others, which are subequal; the fifth reaches beyond the middle of the fourth; the plantar pad is represented by four well-developed contiguous lobes, the inner and outer of which are set rather far back, the greater part of each lying behind the other two. There is no trace of metatarsal pads, the whole area being covered with hair from the heel to the plantar pad. (Text-fig. 54, A, C.)

Judging from Miller's description of the European species *Citellus citellus*, the feet of that species agree tolerably closely with those of *C. beecheyi*. He says, however, that in the fore foot the second and fourth digits are subequal, and that the fifth extends only a little beyond the base of the fourth. This does not apply to *C. beecheyi*. Similarly, he states that in the hind foot of *C. citellus* the fifth digit extends just beyond the base of the fourth, and the hallux not quite to the base of the second digit. This is not true of *C. beecheyi*. But the apparent differences between the two species in the particulars mentioned are interesting, if true, because in the relative length of the digits the typical European species seems to approach the genus *Cynomys*†.

In *Cynomys* the fore foot is long and robust, almost as large indeed as the hind foot. The digits are thick and the claws long. The second digit is a little longer than the fourth, and the fifth reaches a little beyond the base of the fourth. The inner and outer lobes of the plantar pad are small, and together hardly equal the size of the wide median lobe. The outer carpal pad is large and the inner is rather prominent internally, and gives support to the claw of the pollex, which is as long as that of the second digit. The entire sole is naked. In the hind foot the second, third, and fourth digits are subequal, the third only very slightly surpassing the others, as in *Citellus*. The fifth is set almost as far back as the hallux and is only a little longer,

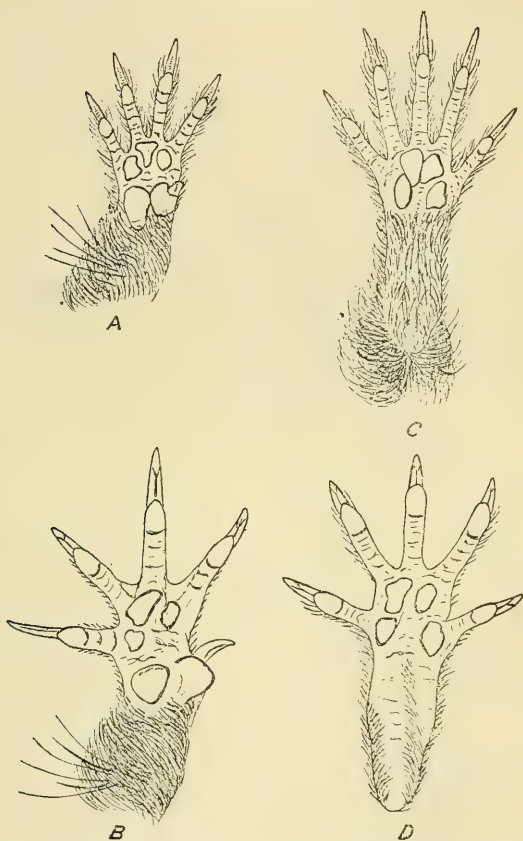
\* A Californian species.

† For a possible explanation of these discrepancies, see note, p. 1208.



surpassing by a little the base of the fourth. The claws on these digits are shorter than on those of the fore foot. There are four well-developed separated lobes constituting the plantar pad, and their arrangement is quadrate, the outer and inner lying behind

Text-figure 54.



- A. Right fore foot of *Citellus* (*Otospermophilus*) *beecheyi*, from dried skin.  
 B. " " " " *Cynomys ludovicianus*.  $\times \frac{1}{4}$ .  
 C. " hind " " *Citellus* (*Otospermophilus*) *beecheyi*, from dried skin.  
 D. " " " " *Cynomys ludovicianus*.  $\times \frac{1}{4}$ .

the others—an arrangement foreshadowed in *Citellus*. There are no metatarsal pads, the sole being naked except for a band of hair passing from the inner side of the heel forwards along the

middle of the metatarsal surface nearly or quite up to the level of the hallucal lobe. (Text-fig. 54, B, D.)

The feet of *Marmota marmota* are relatively more robust and somewhat shorter in the digits than those of *Cynomys*. In the fore foot the three lobes of the plantar pad are relatively larger, occupying practically the entire width of the foot. The carpal pads also are larger, but the inner does not project laterally in the same way and has no trace of the pollex. Similarly, in the hind foot the plantar lobes are massive and do not exhibit that quadrate arrangement seen in *Cynomys* and *Citellus*. Behind the outer lobe of the plantar pad there is a hemispherical external metatarsal, and behind the inner plantar a short internal metatarsal with ill-defined posterior border. (Text-fig. 52, C, D.)

A peculiarity of the feet of this species of *Marmota* is the complete absence of the pollex. Miller noted this in twenty skins, Tullberg's figure showed the same thing, and I have not succeeded in finding a trace of this digit in some half-a-dozen examples I have seen. On the other hand, Miller records the presence of the pollex with a flattened nail in *M. bobak*, the other European species. The presence of a rudimentary thumb is cited by Blanford in his generic diagnosis of *M. himalayana*, *hodgsoni*, and *caudata*, and American writers testify to its retention in *M. monax* and other N. American species.

By the structure of the feet the Marmotine genera may be arranged as follows:—

- a. Feet very powerful; lobes of plantar pads and carpal pads large, metatarsal pads retained.
- b. Pollex suppressed..... *Marmota*.
- b'. Pollex retained..... *Marmotops*\* nov.
- a'. Feet at most moderately powerful; lobes of plantar pads and carpal pads smaller, no metatarsal pads.
- c. Feet comparatively stout, inner carpal pad projecting, a long claw on pollex..... *Cynomys*.
- c'. Feet comparatively slender; inner carpal pad normal; pollex with nail ..... *Citellus*.

*g. Feet of the Flying Squirrels (Petauristidæ).*

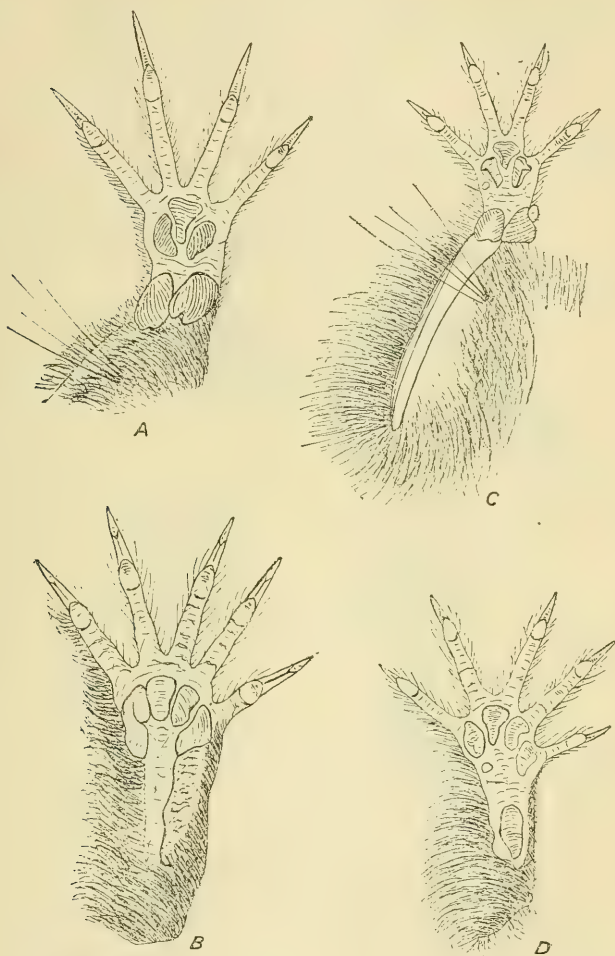
Apart from the cartilaginous rod supporting the patagium and jointed to the wrist just behind the outer carpal pad, the fore feet of the Petauristidæ closely resemble those of the typical arboreal squirrels. In *Petaurista albiventer* (*magnificus*)† the claws are long and strongly curved. The digits also are long and markedly unequal in length, the fourth being considerably longer than the third and fifth, which are subequal and surpass the second. On the specimen examined there is practically no external trace of pollex and none of the nail. The three lobes of the plantar pad and the carpal pads are large and striate all over. (Text-fig. 55, A.)

\* Type, *M. monax*.

† For the specific names here used for *Petaurista* (*olim Pteromys*), see Wroughton, Journ. Bombay Nat. Hist. Soc. xx, p. 1012, 1911.

On the hind foot the claws are similar, but the digits are shorter, the second, third, fourth, and fifth appearing to be nearly

Text-figure 55.



A. Right fore foot of *Petaurista albiventer*, from dried skin.

B. " hind " " " " " " " "

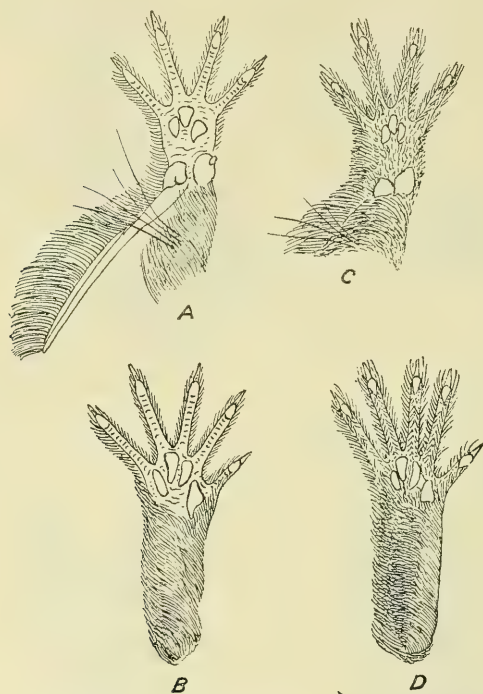
C. " fore " " *Eoglaucomys fimbriatus*, showing the patagial rod.  $\times \frac{1}{4}$ .

D. " hind " " same.

equal, although in reality the fourth is a little longer than the third, which is about equal to the fifth and slightly longer than

the second. The four lobes of the plantar pad are large, the outer and inner being larger than the others. The inner metatarsal pad is well developed, and extends as in *Ratufa* along the inner side of the metatarsal area, being in contact with the plantar pad distally. A large area of the heel is covered with hair, and on the outer side of the foot the hair overgrows the sole up to a line continuous with the proximal extremity of the

Text-figure 56.



- A. Right fore foot of *Glaucomys volans*, summer pelage.  
 B. " hind " " " " " "  
 C. " fore " " " " *stramineus*, winter pelage,  
 D. " hind " " " " " "

large, long, outer plantar lobe, so that the area of naked skin on the admedian side of the metatarsal pad is narrow. (Text-fig. 55, B.)

Blanford described the hind foot of this species, under the name *Pteromys magnificus*, as similar to that of *P. inornatus*, saying of the latter: "The large metatarsal pad joins the inner toe pad. . . . No supplementary pad." This agrees with my

observations; but from the size and length of the outer lobe of the plantar pad I suspect the outer metatarsal pad, referred to by Blanford as the supplementary pad, is retained and fused with it. According to Blanford the feet of *P. yunnanensis* are like those of *albiventer* but larger, whereas in *P. philippensis* (*oral*) there is a large piriform inner and a small outer metatarsal pad, and *P. caniceps* seems to resemble *philippensis* so far as the inner pad is concerned, although Blanford makes no mention of the presence of an outer pad.

In *Eoglaucomyys fimbriatus* the fore foot does not differ materially from that of *Petaurista albiventer* except that there is a distinct pollical excrescence with a nail, as in the typical Sciuridæ, and the plantar and carpal pads carry coarser ridges not distributed all over them but limited to the highest portion of the pads. In some cases there is a little isolated tubercle on the outer side of the external lobe; in other cases this is confluent with the lobe, increasing its width. The hind foot is also tolerably similar to that of *P. albiventer*; the sculpturing of the pads, however, differs as in the fore foot and the inner metatarsal pad, about twice as long as wide, is set at the proximal end of the naked metatarsal area remote from the hallucal lobe of the plantar pad. In this species also, as noticed by Blanford, there is a small circular outer metatarsal pad behind and close to the outer lobe of the plantar pad. If this were enlarged and confluent with the plantar pad, the outer lobe of the latter would resemble tolerably closely that of *Petaurista albiventer*. (Text-fig. 55, C, D.)

None of the other Indian species assigned by Blanford to *Sciuropterus*\* retains the outer metatarsal pad. *S. (Hylopetes) alboniger* has the inner metatarsal pad oval; in *S. (Petinomys) fuscocapillus* it is very elongate; in *Belomys pearsonii* it is oval.

In the North American species, *Glaucomyys volans*, the fore foot structurally resembles tolerably closely that of the Himalayan *Eoglaucomyys fimbriatus*. In a spirit specimen of unrecorded date the underside of the digits and of the entire sole of the foot is naked, whereas in a specimen of *G. stramineus*, which died in December, these surfaces are covered with hair, the pads, which appear to be smaller, alone being naked. The hind foot, however, differs in two correlated characters from that of *Eoglaucomyys fimbriatus*: there is no trace of metatarsal pads, and the metatarsal area is covered thickly with hair from the heel almost to the plantar pad. In the example of *G. volans*, with the naked sole to the fore foot, the undersides of the digits of the hind foot and the area round the plantar pad are likewise naked, whereas in the specimen of *G. stramineus*, with hairy soled fore foot, the lower sides of the digits and the area round the plantar pad are

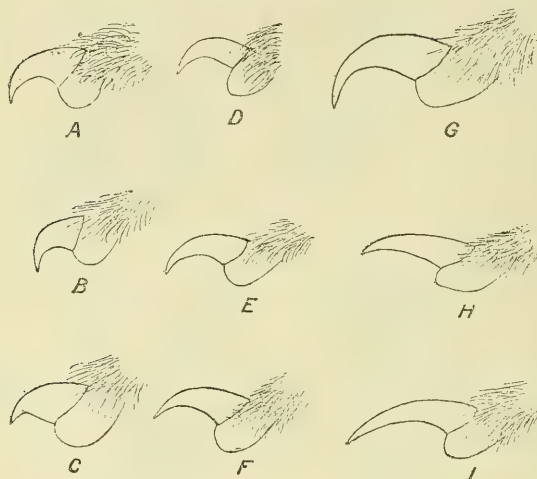
\* For the generic and subgeneric names here used for these species, see Thomas, Ann. & Mag. Nat. Hist. (8) i. pp. 1-8, 1908.



hairy, like the rest of the sole, and the claws are almost concealed. It is probable that the difference between these two closely-related forms in the matter of the hairiness of the soles of the feet is a seasonal difference comparable to that of *Sciurus vulgaris* and of *S. (Tamiasciurus) hudsonicus*. (Text-fig. 56.)

Judging from Miller's description, the feet of *S. russicus*, the type of the genus *Sciuropterus*, closely resemble those of the North American species. It might have been taken indeed from the specimen referred to above as *S. (G.) stramineus*, the soles of the fore foot being thinly haired between the pads, whereas those of the hind foot are covered with a "dense growth

Text-figure 57.



- A. Claw of *Funisciurus leucostigma*; B. *Funisciurus cepapi*; C. *Ratufa indica*; D. *Eutamias quadrivittatus*; E. *Sciurus lindernicus*; F. *Sciurus vulgaris*; G. *Petaurista albiventer*; H. *Citellus beecheyi*; I. *Xerus rutilus*.

of long woolly hairs especially conspicuous along the inner\* side, and adding much to apparent width of foot." Miller had only three specimens of this species for examination, and in the absence of information as to the dates of their capture, it is not possible to guess whether there is a seasonal change in the hairiness of the soles of the feet or not.

To draw attention to the facts here recorded in the hope that they may be amplified and, if necessary, corrected by other

\* For "inner" here read "outer," the error below referred to under *Castor* of confusion between the inner and outer sides of the feet being repeated. The inner side of the foot as generally understood is the side on which the hallux, or first digit, rises, whereas the fringe of hairs on the hind foot of the *Petauristidae* is always on the side of the fifth digit, i. e., the outer.

workers with more and better material, I subjoin the following table :—

a. Metatarsal area hairy, without pads .....	<i>Sciuropterus, Glaucomys.</i>
a'. Metatarsal area partially naked with the inner pad at least retained.	
b. Inner metatarsal pad confluent with plantar pad; pollex practically suppressed, without nail .....	<i>Petaurista albiventer.</i>
b'. Inner metatarsal pad distinct from plantar pad; pollex as in typical Sciuridæ.	
c. Outer metatarsal pad retained .....	<i>Eoglaucomys fimbriatus.</i>
c'. Outer metatarsal pad lost.	
d. Inner metatarsal pad elongate.....	<i>Petinomys fuscocapillus.</i>
d'. Inner metatarsal pad oval .....	<i>Belomys pearsoni, Hylopetes alboniger.</i>

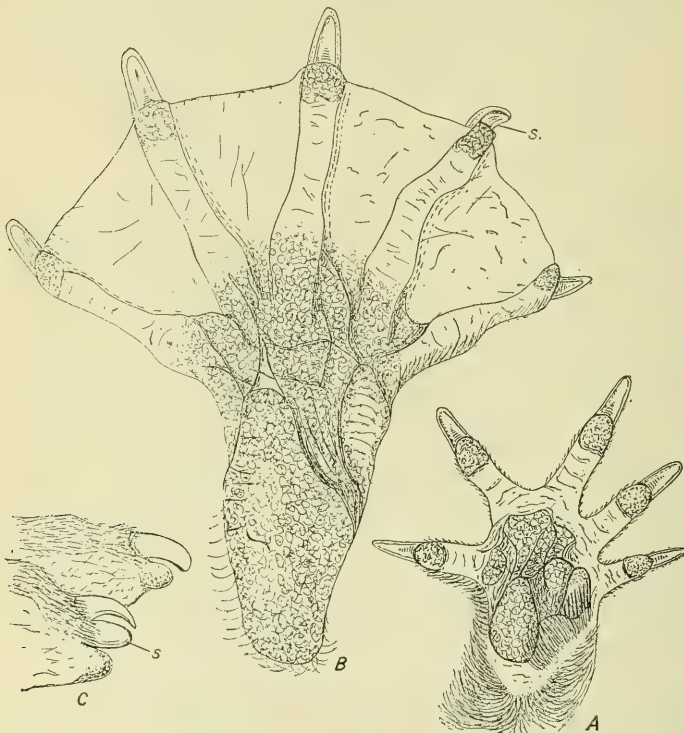
### *h. Feet of the Beaver (Castor).*

Apart from minor differences, the fore foot of *Castor fiber* differs from that of the Sciuridæ and Petauristidæ in two important points, the presence of a well-developed pollex and the indistinctness of the lobes of the plantar pad. The digits are short, with roughened but not well-defined digital pads; the third is the longest, a little exceeding the fourth, the second and fifth being shorter, and the first, or pollex, the shortest of all. All are armed with long, wide, blunt, slightly curved claws, that of the pollex being a little narrower, sharper, and more curved than the rest. The plantar area is granularly reticulated, and the lobes of the plantar pads are obscurely represented by mobile folds of thickened granular skin, hardly alike in any two specimens or even on the two feet of an individual. Only sometimes are the thickenings arranged so as to indicate the three main plantar lobes present in all the Sciuridæ. Behind the plantar area there are two well-developed elongated carpal pads. The inner at the base of the pollex is the smaller, and is hard, smooth, and grooved except at its distal end. The outer pad is much longer and wider, and extends considerably further up the wrist proximally. The comparatively wide space between these pads is occupied by thickened granular skin, which on the admedian side of the inner carpal pad, and a little in front of it, forms sometimes a lobate thickening, which may represent the inner or pollical element of the plantar pad, which should be present with a well-developed pollex, but which is absent in all the Sciuridæ, where the pollex is little more than a vestigial remnant. There is a rim of naked skin behind these carpal pads; but on the inner side of the wrist the hairs are directed obliquely towards the middle line, in a crest overlapping the posterior portions of the pads. There are no carpal vibrissæ, which are present in all Sciuridæ. (Text-fig. 58, A.)

The hind foot greatly surpasses the fore foot in size, far more so than in any member of the Sciuridæ. This is mainly due to

the immense length of the digits, especially of the first and fifth, which, relatively to the other digits, are much longer than in the Squirrels, and give a wide span to the foot. The third and fourth digits are subequal, the fifth is not very much shorter than the fourth and is about equal to the second, and the elongated hallux extends beyond the middle of the second. They are all connected by wide webbing, which extends to the apex of

Text-figure 58.



- A. Right fore foot of *Castor fiber*.  $\times \frac{1}{2}$ .  
 B. " hind " " " "  
 C. Apex of second and third digits of the same, showing the supplementary claw (s) beneath the main claw on the second.

the digital pads or nearly so. These pads are represented by areas of granular skin, and on the first and second digits they form movable lobes, whereas on the third, fourth, and fifth they are less prominent and not separately movable. A well-known peculiarity is the presence of a secondary "false claw" beneath the normal claw of the second digit, constituting with it a fur-

comb, and the claws of the first and second are sharper and more curved than those of the others. The greater part of the lower side of the digits and of the webs is naked, but the proximal ends of the digits and of the webs is thickly granular like the rest of the sole back to the heel. The greater part of the metatarsal area is covered with a big pad extending on the outer side almost as far as the base of the fifth digit, and on the inner side about halfway between the heel and the hallux, where its edge turns obliquely across the sole to meet the outer edge in a widely-rounded curve. This pad is widest across its middle, gradually and slightly narrowed behind and greatly narrowed in front. Between it and the base of the hallux, and separated from it by a narrower or wider furrow, lies a second much smaller pad, the outer edge of which forms the margin of the metatarsal area in front of the inner portion of the larger pad. The distal third of the smaller pad is at the base of the hallux. In front of these pads the skin is folded and grooved, but shows no definite trace of plantar pads. It is difficult to homologize the two pads above described with the pads on the sole of the hind foot in the Sciuridæ. Tentatively I adopt the hypothesis that the smaller inner pad represents the inner or hallucal element of the plantar pad, which is often large in the Sciuridæ, and that the larger pad represents the two normal metatarsal pads fused together and blended with the rest of the integument. The disappearance of the main elements of the plantar pads in *Castor* is in keeping with their partial or complete suppression in other fully web-footed aquatic forms like the Coypu and some others; and the retention of the pads on the metatarsus is to be explained by the beaver's habit of walking on its heels when carrying objects on land. Whether the above suggested explanation be true or not, it is evident that in the structure of its fore and hind feet the Beaver differs greatly from the Squirrels. (Text-fig. 58, B, C.)

My description of the feet was taken from the European species, *Castor fiber*. The American species has similar feet.

Miller's description of the feet of the European species differs materially from mine. The fore foot, according to him, has five palmar tubercles, "the three at bases of median digits large, ill-defined, that at base of thumb not so large as the others but better defined, its outer surface tending to become smooth and horny, the posterior pad largest, covering about one-third of entire palmar surface." It seems clear from this that the inner of the three above-mentioned tubercles at the base of the pollex is the horny grooved pad I identify as the inner carpal pad. If Miller's interpretation is correct, this is the pollical or inner element of the plantar pad. His "posterior pad" must be the large pad I describe as the outer carpal pad.

In his description of the hind foot it is evident Miller has made



the mistake of confusing the first with the fifth digits, for he speaks of the double claw as being on the fourth, whereas it is well known to be on the second digit \*. This makes his description of the proportionate lengths of the digits (and the sizes of their claws) different from mine. Of the pads he says:—"Three elongate ill-defined pads at base of median digits, a larger and better-defined tubercle behind base of hallux [= fifth digit]; entire sole between hallucal tubercle and heel thickened and pad-like."

The characters of the principal types of feet in the Sciuromorpha may be tabulated as follows:—

- |                                                                                                                                                                                                                                                                                                                                                              |                                |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------|
| a. Fore foot with well-developed pollex, lobes of plantar pads reduced to folds of flexible integument, carpal pads very large, no carpal vibrissæ; hind feet with all the digits very long, widely separable and united by webs up to the digital pads; lobes of plantar pad mostly obsolete, greater part of metatarsal area covered by one large pad..... | <i>Castoridæ.</i>              |
| a'. Fore foot with pollex reduced to a mere excrescence or absent; lobes of plantar pads well developed, and as prominent as carpal pads, carpal vibrissæ always present; hind foot with shorter digits, free from webs; plantar pad well developed; metatarsus typically with two pads, a longer inner and a smaller outer, both sometimes suppressed       |                                |
| b. A carpal rod supporting patagium, digits as in arboreal Sciuridæ .....                                                                                                                                                                                                                                                                                    | <i>Petauristidæ.</i>           |
| b'. No carpal rod.                                                                                                                                                                                                                                                                                                                                           |                                |
| c. Fourth digit the longest, much longer than the second.....                                                                                                                                                                                                                                                                                                | <i>Sciuridæ</i> (arboreal).    |
| c'. Third digit the longest, fourth not much longer than second .....                                                                                                                                                                                                                                                                                        | <i>Sciuridæ</i> (terrestrial). |

### *The Anus and External Genitalia.*

In the *Sciuridæ* and *Petauristidæ* the anus and external genitalia are normally separated. In the male the prepuce † is prominent and situated some distance in advance of the anus, being mostly long and pendulous and even retroverted, when at rest, in the arboreal Squirrels, the Bristly-Ground Squirrels, and the Flying Squirrels, but shorter in the Marmots. Between it and the anus there is in the Squirrels a very large scrotum in the breeding season, but I have not been able to verify this in the case of the Marmots. In the female the vulva is a semi-circular or pointed process, situated a little below the anus, and the clitoris is concealed within the labia. The anus has the two normal glands in the Squirrels, whereas in the Marmots there is an additional median gland. (Text-fig. 59, A, B, C.)

The anus and external genitalia in *Castoridæ* differ profoundly from those of the *Sciuridæ* and *Petauristidæ*.

Externally the male and female are alike, owing to the orifices of the alimentary canal and of the genito-urinary organs

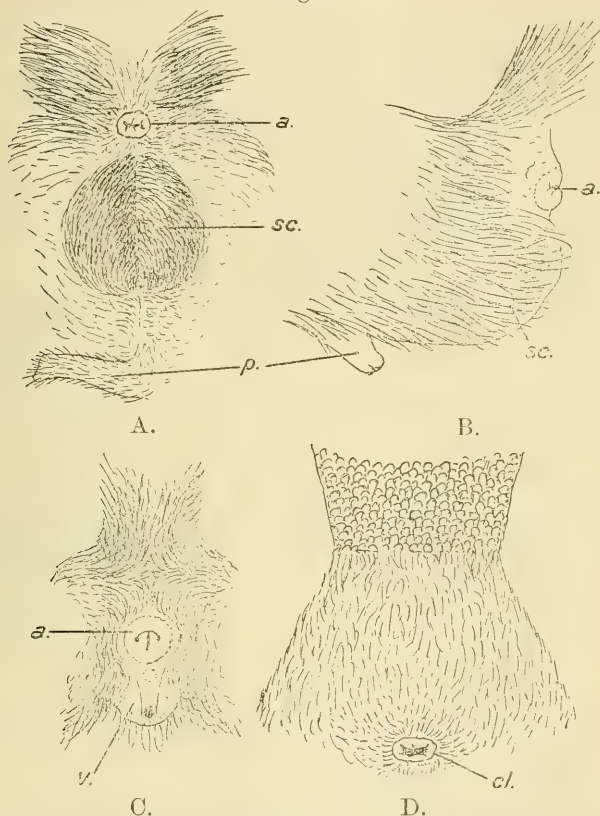
\* This error no doubt arose from the fashion now in vogue of twisting the hind feet in made-up skins so that the hallux lies on the outer side of the foot so placed.

† The structure of the penis and *baculum* I must leave for another paper.



discharging into a common chamber or cloaca, the aperture of which, closed by a sphincter muscle, is placed at the base of the thick hairy portion of the tail. In the male, moreover, there is no scrotum, the testes being inguinal in position, that is to say, beneath the integument covering the pubic portion of the pelvis. (Text-fig. 59, D.)

Text-figure 59.



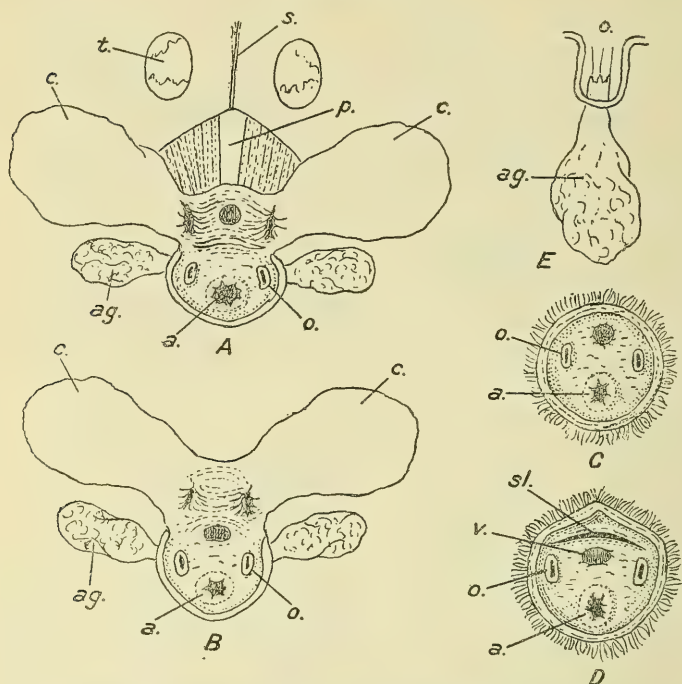
- A. Anal and genital region of male of *Callosciurus prevosti*, from below.  
 B. The same of *Geosciurus capensis*, from the side.  
 C. " " " female *Cynomys ludovicianus*.  
 D. " " " male or female *Castor fiber*.

a, anus; sc, scrotum; p, prepuce; v, vulva; cl, orifice of cloaca in *Castor*.

When the cloaca of the male is opened, four orifices, two median and one on each side, are seen to open into it. The posterior and larger median orifice is the anus, the anterior and smaller median orifice is the common aperture of the penis and the castorium glands. The paired orifices, one on each side and

remote from the anus, are the apertures of the anal glands. Each of the apertures of the anal glands leads into a deep narrow pouch, at the bottom of which are three papillæ, each tipped with a long hair. This pouch can be evaginated, so that the gland comes to the surface, and the strong-smelling secretion

Text-figure 60.



- A. Diagrammatic dissection of the anus and genitalia of male *Castor canadensis*.  
 B. The same of the female.  
 C. The cloaca of the male, opened.  
 D. " " " " female "  
 E. One of the anal glands, showing the tip with its papillæ and setæ within the pouch.

*t*, testis; *s*, pubic suture; *p*, penis; *c*, castorium glands with orifices on each side of preputial orifice in male and above vaginal orifice in female; *v*, vaginal orifice; *ag*, anal gland; *o*, orifice of anal gland; *a*, anus; *sl*, slit through which secretion of castorium glands is discharged into cloaca in female.

is discharged at the tips of the papillæ. Normally the penis is completely retracted, but it is capable of being protruded through the orifice above mentioned into the cloaca and thence to the exterior. Through this orifice the secretion of the castorium

glands is also discharged. These are represented by a pair of immense sacs, with puckered walls, one lying on each side. They are filled with fluid; and the aperture of each sac opens close to the median aperture of the penis, the three apertures lying close together just within the common orifice above mentioned. (Text-fig. 60, A, C, E.)

The arrangement is very similar in the female, in which the anal and castorium glands appear to be as well developed as in the male. The chief difference is that the orifice of the vagina opens separately into the cloaca. Just in front of it there is a transverse slit in the wall of the cloaca, and when this is opened the apertures of the castorium glands may be seen on each side of it, just in front of that of the vagina. (Text-fig. 60, B, D.)

To sum up, the Castoridæ differ from the Sciuridæ, so far as the organs just described are concerned, in the following particulars:—(1) In both sexes the anus and genitalia open into a common chamber or cloaca with a single external orifice. (2) The anal glands are of great size and open apart from the anus. (3) There is a pair of large castorium glands opening close to the generative orifice. (4) In the male there is no scrotum; the penis is straight and is protruded close to the anus.

In view of these well-known and profound differences, it is singular that in the current text-books the Castoridæ are separated from the Sciuridæ merely by such comparatively trivial differences as are presented by the skull and teeth, the webbed hind feet and broad tail being added as of secondary value, and no mention whatever being made of the genitalia and anus. The difference between the Beavers and Squirrels in the anus and external genitalia may be summarized as follows\* :—

- a. Sexes externally alike owing to the anus and genito-urinary orifices opening into a cloaca with a single aperture at the root of the tail, no hairy prepuce or vulva, the concealed orifice of the penis just in front of the anus; testes inguinal; a voluminous "castorium" gland opening close to the orifice of the penis and vulva; anal glands very large, with long tubular orifice..... *Castoridæ.*
- b. Sexes externally unlike, the anus and external genitalia not opening into a cloaca; female with hairy vulva close beneath anus; male with long perineal region, typically with large scrotum for testes in breeding season; penis long, opening by prominent hairy prepuce on posterior part of abdomen; no "castorium" gland; anal glands small, with small orifice.

*Sciuridæ, Petauristidæ.*

From the above-given analyses of the external characters of the Castoridæ, Sciuridæ, and Petauristidæ it will be seen that, so far as the organs considered are concerned, there is not a particle of evidence of kinship between the Castoridæ and the other two families.

\* I have not in this paper dealt with the great differences between the Beavers and Squirrels in the tail, because they are well known.

If the structural differences between the Flying Squirrels and the less specialised true Squirrels entitle these groups to be regarded as distinct families, the differences between the Beavers and the Squirrels must be granted much higher rank. The Sciuridæ and Petauristidæ may be associated as the Sciuroidea, and the Beavers kept apart as the Castoroidea. The Petauristidæ are a compact group represented by several genera and subgenera; but, so far as my limited observations on the external characters are concerned, I have found no reasons for thinking them susceptible of grouping under headings of subfamily rank. The genera of Sciuridæ are much more varied; but their affinities are at present too little understood to warrant the subdivision of the family.

53. On the Morphology of the Chondrocranium of the Larval Herring (*Clupea harengus*). By F. R. WELLS\*.

[Received October 18, 1922: Read November 21, 1922.]

(Text-figures 1-11.)

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## 1. INTRODUCTION.

This research was started at the suggestion of Prof. MacBride, the work being carried out in his laboratory in the Imperial College of Science, our attention being drawn to the necessity of studying the development of the chondrocranium, in particular, of the more primitive Teleostei by work being done by Mr. Norman on the Eel, which, like the Herring, has no upper jaw in the early larval stages.

The paper refers to the larvæ of the Clupeoid, *Clupea harengus*: all observations and reconstructions were made from these only, although the internal morphology of the Sprat and Pilchard was found to be indistinguishably similar. The paper describes only the chondrocranium. For convenience, the larvæ have been divided into stages as follows:—5 mm., 10 mm., 20 mm., 30 mm., and metamorphosing stages (40 mm. and 50 mm.).

Previous work on the skulls of Teleostomi includes the following:—Salmon (Parker, 1872; Stöhr, 1882; Gaupp, 1903; Boker, 1913), Trout (Winslow, 1897), *Gasterosteus* (Swinerton, 1920), *Cyclopterus* (Uhlmann, 1921), *Syngnathus* (McMurrich, 1884), *Amiurus* (Kindred, 1919), Selachian (Parker, 1879; Sewertzoff, 1899), Chondrostei (Parker, 1883; Sewertzoff, 1902), *Lepidosteus* (Parker, 1883; Veit, 1911), and a recent paper on *Amia* (Pehrson, 1922), in which is pointed out the need for the study of the morphogenetic development of the cranium of the

\* Communicated by Prof. E. W. MACBRIDE, F.R.S.



Teleostei, more especially of the Clupeidæ and Siluridæ. No work has been done on the cranial development of the former\*.

Material was obtained from Plymouth, and was fixed on the trawler as it was caught; the larger stages were caught in Dublin Bay in 1921; material was also obtained from Lowestoft.

I wish to thank Prof. MacBride, Dr. Hogben, and Mr. H. Graham Cannon for valuable suggestions and assistance with both the work and the manuscript.

## 2. METHOD.

The specimens were fixed in Bouin's fluid, in Chromic-Urea-Bouin, or in Corrosive Sublimate. The first was found to be most successful. A number of series of transverse sections were cut, at  $8\frac{1}{2}\mu$ ; they were then stained in Ehrlich Hæmatoxylin, in Borax Carmine and Picronigrosine, in Mallory's triple stain, or in Thionin and Orange G. The last was found to be the most successful.

The usual wax model method of reconstruction was not used. The reconstructions were made direct as dorsal or lateral views on specially squared paper. The exact method is as follows:—

An eyepiece micrometer, divided into squares, was used. The virtual size of these squares, with the various powers used, was measured by means of a blood-corpuscle measuring slide divided into hundredths of a blood millimetre. With the microscope used (Leitz, eyepiece 3, objective 3, draw-tube 140) one square was found to measure  $\cdot 15$  mm. The reconstructions were made at a magnification of 120. The paper was therefore "squared" with lines 18 mm. apart vertically (or longitudinally) and 1 mm. apart ( $= 120 \times 8\frac{1}{2}\mu$ ) horizontally (or transversely). The direction of the lines on the micrometer was then set according to the direction from which the view was taken, and the reconstruction mapped out directly on to the squared paper. This method is really a simplification of the method, which was tried at first, of drawing each, or alternate, section on squared paper and then reconstructing dorsal or lateral views by measuring these drawings. The new method merely eliminates the intermediate process. It was found to be very considerably quicker, and certainly as accurate as the wax model method. The same assumption had to be made as is made in the model method—that is, the assumption that one of the cartilages was straight. In the reconstructions made the ethmoid plate was taken for

\* It is interesting to note that none of the above-mentioned types have larvæ, as do the Clupeoids, Flat-fish, &c. The term "larva" is here taken to refer to the free-swimming stage preceding metamorphosis as opposed to the newly-hatched yolk-sac bearing embryo. Lebour and others refer to this free-living stage as the post-larval stage.

this centre; corrections to allow for this can quite easily be made from longitudinal sections of a similar larva. To make comparison more easy and more accurate, all reconstructions were made to the same scale, using the same micrometer and microscope.

### 3. EXTERNAL CHARACTERS.

The specimens examined varied in length from 5 to over 50 mm.; the 10 mm. stage was taken in the greatest detail, and it corresponds to an age of less than a month. The larvæ were of the Herring, distinguished from those of the Pilchard and Sprat, as is pointed out by Fage (1920), by the number of myotomes, having 56 to 58, 51 to 52, and 46 to 48 respectively.

The tail is characteristically short, the anus being very close to the end of the body. In a specimen 10.5 mm. long we have the following measurements:—head 1.5 mm., trunk 7.5 mm., tail 1.5 mm. (Lebour, 1921). The head is nearly as broad as it is long (including the eyes), the lower jaw protruding forwards well beyond the upper.

The only visible fins at first are the pectoral and caudal, the pelvic fin not appearing until a length of over 20 mm. is reached, and the dorsal fin is not complete until the animal is 28 to 29 mm. long (Lebour, 1921).

None of the specimens of 10 mm. upwards examined had the yolk-sac still present, although it may persist until 12 mm.

These and other points have been illustrated in text-fig. 1.

Metamorphosis takes place at about 40 mm.

### 4. DISCUSSION.

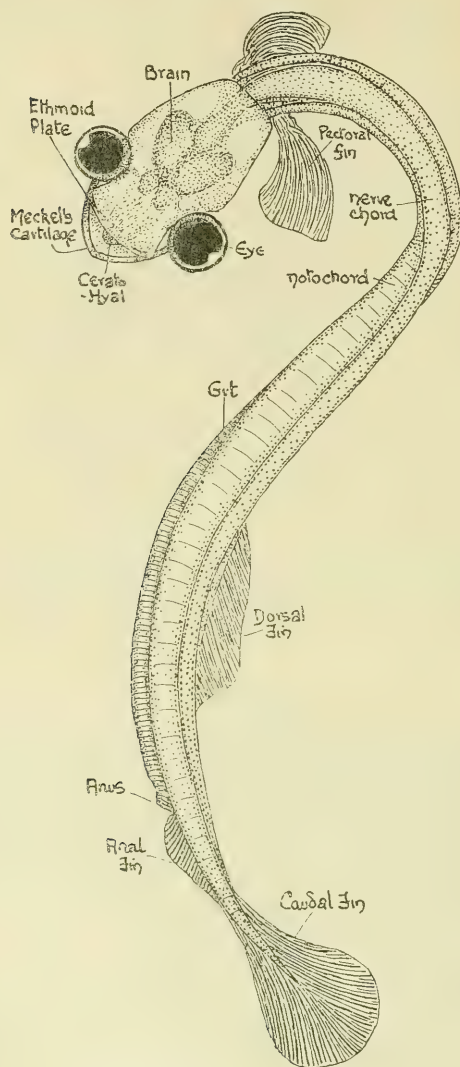
This research, as stated in the Introduction, was carried out to fill a very noticeable gap in the work done on the development of the Teleostean chondrocranium. The paper does not pretend to be a complete account, and it has very little detail in it; the results obtained were so unexpected and abnormal that I have made no attempt to explain or to theorise. Time was unfortunately too short for me to make it a comparative account; it is, in fact, merely a simple description of the state of affairs found.

The first striking point is this: there is in the early stages no upper jaw at all—it does not appear until the larva attains a length of about 13 mm.

Another point is that at the earliest stage examined (*i. e.* 5 mm.) the hyomandibular mass of cartilage is fused both to the cranium and to Meckel's cartilage. It breaks away from the first at about 15 mm., and the second at 25 mm. The upper jaw grows back, and fuses with it secondarily. The quadrate is formed from this mass by a constriction forming in it.

It is interesting that the larvæ showed points of interest not only in the chondrocranium. The development of the pituitary

Text-figure 1.



Larval *Clupea harengus*. 15 mm. Stage.

body does not tally exactly with the previous accounts. This matter was briefly examined, and will be published separately.

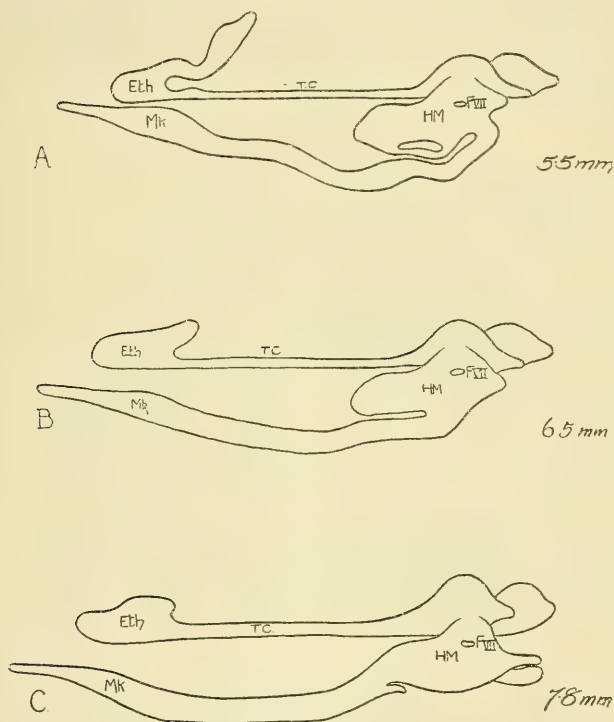
## 5. THE CHONDROCRANIUM.

a. *The 5 mm. Stage.*

This description is based on the study of transverse sections of a specimen nearly 5.5 mm. long. Sections, for confirmation and comparison, of slightly longer specimens were also cut (text-fig. 2).

In front, the chondrocranium is a thin plate of cartilage, in the form of a deep, nearly straight-sided trough, about half as deep

Text-figure 2.



Lateral views of early stages of Larval Herring.  $\times 120$ . From reconstructions.

as it is broad. A little further back the sides turn up, and separate from the median part forming large upturned processes, which lie on each side between the brain and the eyes. The median part becomes a somewhat narrower nearly flat plate, which soon divides into two narrow processes enclosing a large foramen in which the pituitary lies. These enclosing processes are the Trabeculae Cranii.

At the posterior end of this foramen the processes widen laterally and turn up sharply. The median part forms a tube enclosing the notochord.

From near the top of the lateral upturned process there grows down a cartilage, laterally thin, which soon elongates to form a large flat plate, slating out at the top. This is the hyomandibular. Close below its fusion with the cranium there is a foramen, of the hyoid branch of the VIIth (facial) nerve.

At the bottom of this plate and slightly in front of its fusion with the cranium there is a narrow elongated slit. From the posterior end of this hyomandibular there grows downwards and forwards a thin cartilage. This runs along the lower side of the hyomandibular, and then forwards and upwards. The halves (it is, of course, like the hyomandibular, paired) meet some way in front of the anterior end of the ethmoid plate; they are not fused, but articulate.

(The naming of the cartilages is based on study of later stages.)

There is at this stage *no trace of an upper jaw* (i.e. the palatal, pterygoid, and quadrate cartilages), the only roof to the mouth being the ethmoid plate.

A specimen of 6.5 mm. was examined, and showed only a few slight differences; the large upturned processes are distinctly smaller, and the narrow elongated slit in the hyomandibular mass is closing up. The fusion of this mass with Meckel's cartilage is still placed as in the younger stage.

In a 7.5 mm. specimen it was found that the large upturned processes had diminished considerably in size, being very little larger, comparatively, than in the 10 mm. stage. The narrow elongated slit in the hyomandibular has entirely closed up, and the fusion of the posterior process from Meckel's cartilage to the hyomandibular has moved forwards, being now situated directly below the anterior end of the fusion of the latter to the cranium.

Text-fig. 2C shows a reconstruction of a 7.8 mm. specimen; the upturned processes have disappeared entirely, and the fusion of Meckel with the hyomandibular has moved right forwards to the anterior end of the latter, and its fusion with the cranium is as before.

#### b. *The 10 mm. Stage.*

This description of the chondrocranium is based on the study of transverse sections in all nine series, on whole mounts of specimens of *Clupea harengus* varying in length from 9 to 11 mm., and on reconstructions made from a 10 mm. specimen (text-figs. 3 & 4).

In front the ethmoid plate is still thin, but it has flattened out considerably, being at first dorsally convex and, further back, concave. In front this ethmoid plate is very broad, measuring nearly .5 mm. across; it runs back for nearly one-third of the length of the head before dividing to give off the

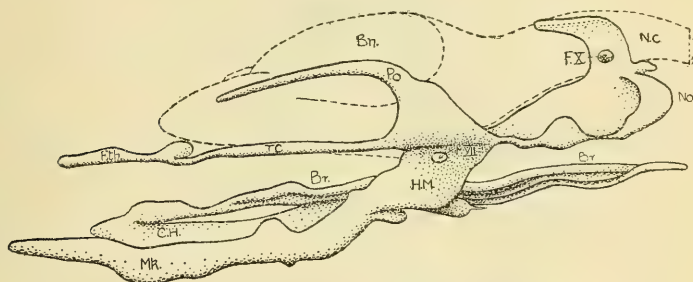


Trabeculæ Cranii. The pituitary foramen is now about .45 mm. long and half as wide. Just anterior to the posterior end of this foramen these processes (the Trabeculæ Cranii) widen laterally as before, and turn up sharply to send forwards the long, slender post-orbital processes. (These might also be called the supra-orbital processes, but the former name is chosen as it emphasises the fact that they grow forwards from behind, and that they lie between the eyes and the brain and not over the eyes.) Small protrusions, corresponding to the large upturned processes of the 5 mm. stage, turn back from the ethmoid plate as if to meet these post-orbital processes. The orbit is thus, at this stage, incomplete, as it is in the 10 mm. *Syngnathus*, whereas in the 8 mm. *Amiurus* and the second week *Salmo* it is complete.

In the flat plate between the pituitary foramen and the post-orbital processes are the foramina of the VIIth nerve.

The anterior end of the notochord lies directly behind the pituitary foramen, and it is enclosed in cartilage for the first

Text-figure 3.



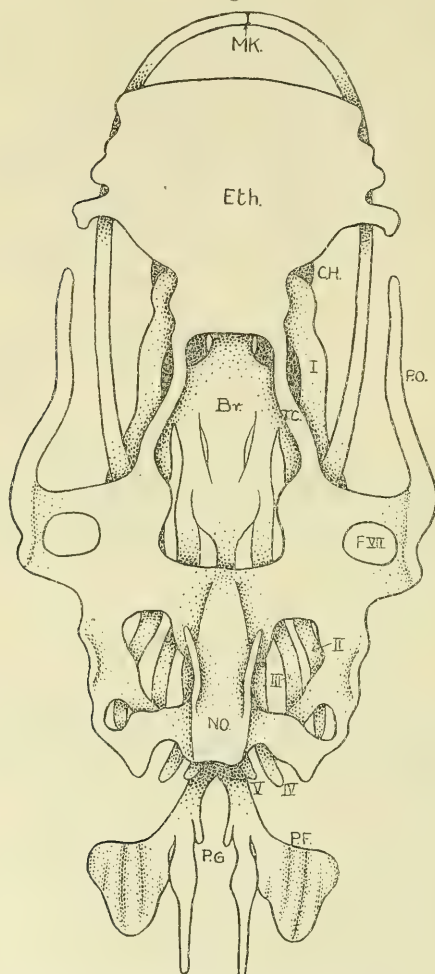
Lateral view of chondrocranium. 10 mm. Stage. X 55.

.5 mm. of its length. On each side of this are the auditory capsules, enclosed at their posterior end by cartilage. The brain and nerve-cord are in no place completely roofed over, the nearest approach to this being two thin, high processes lying laterally to and nearly level with the top of the nerve-cord; these arise from the cartilage enclosing the notochord, near the posterior of the head. In them is the foramen of the Xth nerve (vagus). The 10 mm. *Syngnathus*, 8 mm. *Amiurus*, and second week *Salmo*, all have the posterior end, at least, of the brain roofed over.

At this stage there is still no trace of an upper jaw. Meckel's cartilage protrudes conspicuously beyond the ethmoid plate; the two halves are narrow but deep. The jaw widens rapidly until it is nearly as wide as the ethmoid plate, and then narrows slowly until it meets the hyomandibular. The two are still definitely fused, Meckel's cartilage extending as a long forward growth from the anterior end of the hyomandibular.

The hyomandibular is a great mass of cartilage, sloping backwards and outwards at the top and measuring about .5 mm. long, .15 mm. deep, and nearly .1 mm. broad. It meets the cranium just behind the post-orbital processes and between the

Text-figure 4.

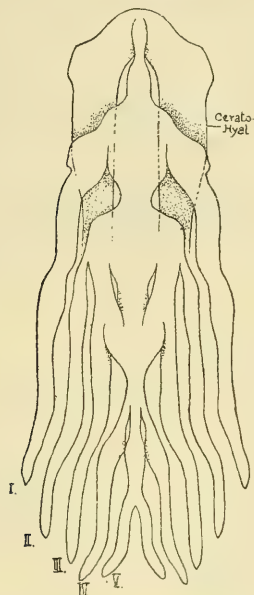
Dorsal view of chondrocranium. 10 mm. Stage.  $\times 70$ .

foramina of the VIIth nerve and the pituitary. The hyomandibular touches the cranium for about half its length, being articulated in front and fused behind.

The foramen of the hyoid branch of the VIIth (facial) nerve is situated as in the 5 mm. stage.

At the posterior end of the hyomandibular, at the bottom, there articulates with it the ceratohyal, by means of a conspicuous knob, probably the appearing stylohyoid, as in *Syngnathus*.

Text-figure 5.



Dorsal view of branchial arches. 10 mm. Stage.  $\times 60$ .

The ceratohyal runs forward as far as the anterior end of the ethmoid plate; arising from the anterior end of the ceratohyal are the branchial arches.

The accompanying figure is of the branchial arches of a larva at this stage; the figure is self-explanatory.

c. *The 20 mm. Stage.*

This description is based on reconstruction of a 20 mm. specimen of *Clupea harengus* (text-fig. 6)

At its extreme anterior end the ethmoid plate is, as in the 10 mm. stage, a flat plate; a little further back a median dorsal ridge appears. This ridge runs back as far as the two lateral protrusions, which are considerably developed.

The ethmoid plate now becomes comparatively thinner; the pituitary foramen is also comparatively smaller. The post-orbital processes are thicker, and run forwards beyond the lateral

protrusions and come down close to the median ridge. About half-way along these post-orbital processes a bridge is formed between them, which gives off two median thin processes, one forwards and one backwards. This bridge roofs over part of the anterior end of the brain (epiphysial bar).

Arising from the anterior end of the upturned sides of the ethmoid plate, from which the post-orbital processes arise, are paired backward growing pieces of cartilage; these meet processes growing up from the sides of the posterior end of the ethmoid plate, and enclose the anterior end of the auditory capsules. From the top of these a bridge grows to cover part of the posterior end of the brain. The posterior end of the auditory capsules is enclosed as in the 10 mm. stage. The cartilage enclosing the notochord is as before.

Articulated with the sides of the anterior end of the ethmoid plate are small paired cartilages—the early beginnings of the upper jaws (the palatal part of it). This appears first at about 13 or

Text-figure 6.



Lateral view of chondrocranium. 20 mm. Stage.  $\times 40$ .

14 mm. They run back as far as the anterior end of the pituitary foramen. They have no connection whatever with either the hyomandibular or with Meckel's cartilage. This is very similar to the 10 mm. *Amiurus*, in which the palatal arises separately close to the ethmoid plate and the pterygo-quadrate grows forwards from the hyomandibular to meet it. At this stage, however, there is no trace of any forward growth from the hyomandibular. The palatal arises separately similarly in *Syngnathus* (8 mm.).

The hyomandibular is articulated with the cranium, and in no place is it fused with it; it is a considerably larger mass of cartilage, comparatively, than in the 10 mm. stage. The part articulating with the ceratohyal has grown back and away from the main mass, forming even more conspicuously a stylohyoid cartilage. Anterior to the base of this process a long pointed piece of cartilage grows forwards.

The hyomandibular is considerably elongated, and there is a

slight restriction where it meets Meckel's cartilage. At the lower part of this restriction the two cartilages are divided to indicate a coming division between them.

Meckel's cartilage is very much as in the smaller 10 mm. stage, wide at the base and tapering to a thin, horizontally flattened cartilage at its anterior end.

The two foramina of the VIIth, facial, nerve (*i.e.* in the hyomandibular and in the ethmoid plate) are unchanged.

#### d. The 30 mm. Stage.

The following description is based on the study of transverse sections of a 30 mm. specimen of *Clupea harengus* and on a reconstruction of it (text-fig. 7).

The median ridge in this stage runs to the extreme anterior end of the ethmoid plate, the top bulging laterally considerably; near the posterior end of this ridge it divides to enclose the anterior end of the brain. Just below the top bulge there is the foramen of the 1st nerve.

Text-figure 7.



Lateral view of chondrocranium. 30 mm. Stage.  $\times 20$ .

The ethmoid plate runs back from this at first as in the previous stage, being nearly flat. It then tapers to a long median point, on each side of the base of which are slight knobs, the remains of the Trabeculae Cranii, which are now absent. A ventral view of this is shown in text-fig. 8.

From the cartilage enclosing the anterior end of the brain the paired post-orbital processes extend back as before. The bridge over the brain and between these (the epiphysial bar) is unchanged. From the posterior end of this bar there runs a process, along the top of the brain, to meet the cover to the posterior end of the brain.

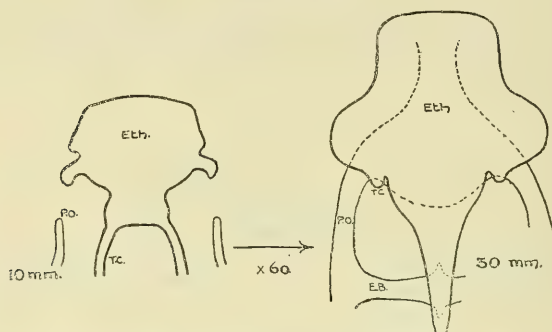
The auditory capsules are now completely enclosed by cartilage. The processes which in the 20 mm. stage grew back from close behind the post-orbital processes are now broken, to give long sloping slits in the upturned sides of the ethmoid plate. Part of the posterior end of the hind brain and the anterior end of the nerve-chord are entirely roofed over by cartilage.



The palatal cartilage is comparatively larger in cross-section, and from its posterior end there runs a thin strip of cartilage to meet the hyomandibular mass at its anterior end. It is important to notice that this fusion is entirely secondary, and, as pointed out above, the upper jaw grows *back* from the front.

The hyomandibular mass of cartilage has grown considerably, being now nearly half as long as the whole chondrocranium. The articulation with the cranium is as before, the stylohyoid and the forward growing piece of cartilage, just in front of it, are even more conspicuous. Just in front of the base of this forward growing part the hyomandibular mass forms a narrow neck, and

Text-figure 8.

Ventral views of ethmoid plate in the 10 mm. and 30 mm. Stages.  $\times 30$ .

spreads out again further forward. From its anterior end on top it sends forward the thin strip to meet the upper jaw, and immediately below this there is a small protrusion which articulates with Meckel's cartilage. At the articulation there is a large upward growth from Meckel's cartilage, otherwise it is unchanged.

The two foramina of the VIIth nerve (facial) are unchanged.

e. *The 40 mm. Stage.*

This account is based on the study of transverse sections of a 40 mm. specimen of the Herring and on a reconstruction of it (text-fig. 9).

The whole chondrocranium has considerably increased in height without a very marked change in length.

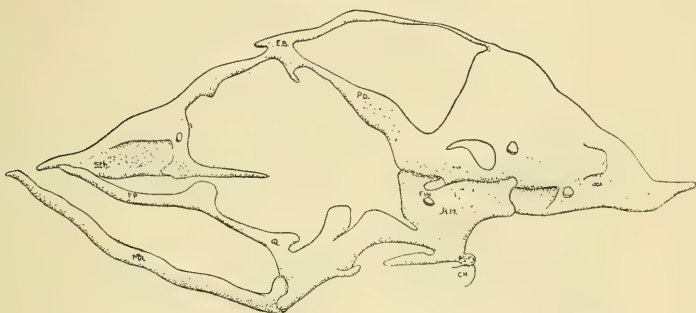
The anterior end of the ethmoid plate and the median ridge show little change, except in the formation of the anterior eye-muscle canal; the rostrum is more pointed. The epiphysial bar is unchanged; the post-orbital processes have become comparatively more massive, and from the ventral side of their anterior

end a pair of small backward-growing protrusions have appeared. The median process running along the top of the brain is very much thinner, especially near the posterior end.

The long sloping slits in the upturned sides of the posterior part of the ethmoid plate—mentioned as present in the 30 mm. stage—are now closed at the upper and anterior end, leaving a large foramen. The roof over the posterior end of the brain is now complete.

The anterior end of the palato-pterygoid is practically unchanged, the posterior end being somewhat enlarged to form an upturned knob. There is a slight restriction where it meets the hyomandibular mass.

Text-figure 9.



Lateral view of chondrocranium. 40 mm. Stage.  $\times 20$ .

The articulation of the hyomandibular with the cranium is no longer complete, being broken in the middle. The hyomandibular mass has changed very considerably—changes which are even more marked in the 50 mm. stage,—and it is perhaps best to describe them in the next section.

Considerable ossification is commencing.

f. *The 50 mm. Stage.*

[See text-figure 10.]

The nasal septum appears at this stage at the base of the rostrum; apart from this the anterior part of the ethmoid plate remains unchanged. The post-orbital processes are again more massive, and the process running medianly from the epiphysial bar to the posterior end of the cranium is, as it originally was, incomplete.

The retro-articular process on Meckel's cartilage is now conspicuously developed.

No other differences have appeared except in those cartilages concerned in the suspension of the jaws.

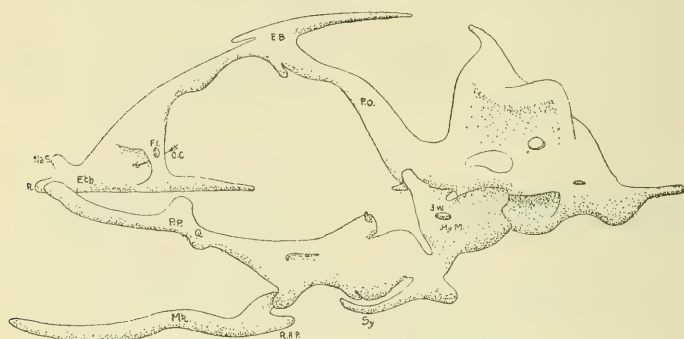
Text-fig. 11 shows the suspensory apparatus of *Clupea harengus* and of *Amia calva* (from Torsten Pehrson, 1922) for

the purpose of naming the various cartilages present. The explanation offered in the figure does not explain the slight constriction in the middle of the quadrate.

It remains, however, without doubt that the quadrate, the symplectic, stylohyoid, hyomandibular, and Meckel's cartilages, all arise from the same single mass of cartilage, which mass was originally fused to the cranial part of the skull, whereas the palato-pterygoid cartilage arises entirely separated.

Text-fig. 11 shows the development of the suspensory arrangement of the jaws compared with that of *Amia calva*, and also

Text-figure 10.



Lateral view of chondrocranium. 50 mm. Stage.  $\times 17$ .

stages in *Salmo* and *Syngnathus*. This figure tends to fill in the gap left by the absence of any comparison in the text.

To assist further comparison, the following table, showing the rate of growth of the larva, is given :—

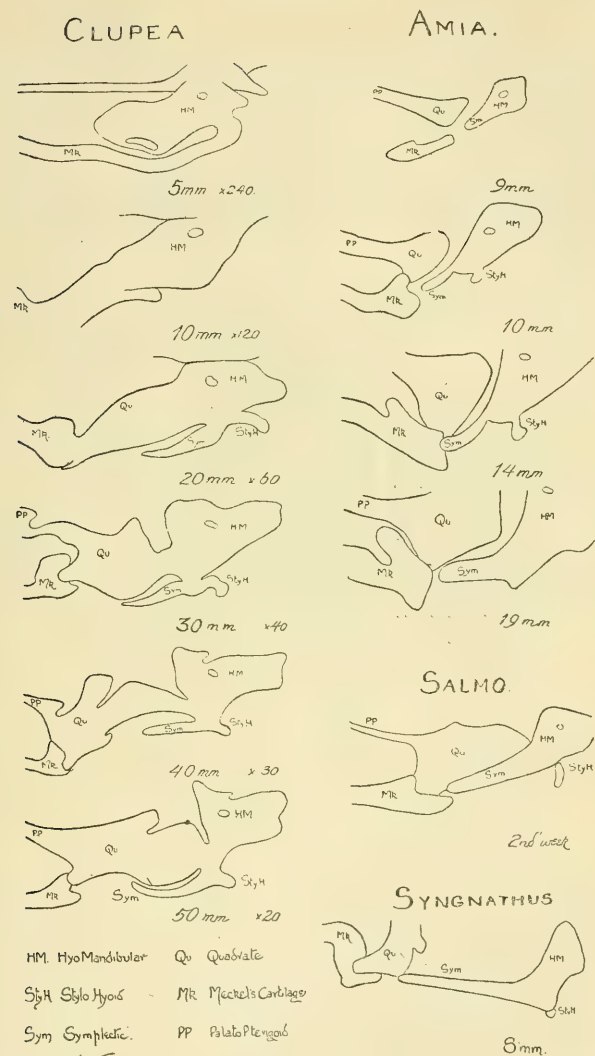
Hatching .....	4 mm.
2 weeks .....	10 mm.
1 month .....	18 mm.
2 months .....	35 mm.
3 months .....	48 mm.
4 months .....	55 mm.
	approx.

(H. A. MEYER.)

## 6. SUMMARY.

1. The hyomandibular, quadrate, symplectic, and stylohyoid are, in the 5 mm. stage, all one mass of cartilage.
2. This mass is fused, at this stage, to the cranial cartilage and to Meckel's cartilage.
3. The palato-pterygoid forms at about 13 mm., and grows back to meet the quadrate.

Text-figure 11.



7/11/22 *Sp*  
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Diagram comparing development of suspensory apparatus of jaws of *Clupea*, *Amia*, *Salmo*, and *Syngnathus*. Reduced one-half from dimensions printed on block.

4. Until the 20 mm. stage is reached, the brain is in no place roofed over.
5. The Trabeculæ Cranii disappear between 20 mm. and 30 mm., leaving a median process, which does not join the posterior part of the skull.
6. The quadrate appears by a constriction in the hyomandibular mass.
7. The symplectic appears as a thin pointed process from beneath this mass.
8. Articulations of this mass with the cranium and with Meckel's cartilage appear at 10 mm. and 26 mm. respectively.
9. Considerable ossification is taking place at 30 mm.

#### 7. LIST OF ABBREVIATIONS USED IN THE ILLUSTRATIONS.

Br. ....	Branchial arches.
C.H. ....	Ceratohyal.
E.B. ....	Epiphysial bar.
Eth. ....	Ethmoid plate.
F.etc. ....	Foramen of I(etc.) nerve.
H.M. ....	Hyomandibular.
Mk. ....	Meckel's cartilage.
NaS. ....	Nasal septum.
N.O. ....	Notochord.
P.F. ....	Pectoral fin.
P.G. ....	Pectoral girdle.
P.O. ....	Post-orbital process.
PP. ....	Palato-pterygoid cartilage.
Qu. ....	Quadrate.
R. ....	Rostrum.
RaP. ....	Retro-articular process.
StyH. ....	Stylo-hyoid.
Sy. ....	Symplectic.
T.C. ....	Trabeculæ Cranii.

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54. On the Colours of Water-Mites. By C. S. ELTON,  
New College, Oxford \*.

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1. INTRODUCTION.

There are in the British Isles over 250 species of Hydrachnidæ or Water-mites, belonging to about 40 genera [7]. The life-history is interesting, as the larva is usually parasitic upon some other fresh-water animal (e. g., *Hydrachna globosa* or *Dytiscus*, *Nepa*, etc.), although the adult is free-living. By such means dispersal is often effected. One result of this rather elaborate and risky life-history is that comparatively few adults are usually found. We should expect, *a priori*, to find some special method of defence among these mites, since they are not able to increase rapidly in numbers, in order to counteract the deprecations of enemies.

The colours of Water-mites are very varied. As this paper deals mainly with the scarlet species, the genera may be roughly divided into four groups in order to give some idea of the colours which occur :

1. All the species of the genus bright red, e. g., *Eylais*, *Diplo-dontus*, *Hydryphantes*, etc.
2. Most of the species of the genus bright red, but a few non-red, e. g., *Hydrarachna*.
3. A few of the species of the genus bright red, but most of them non-red, e. g., *Limnesia*, *Arrhenurus*, *Piona*.
4. All the species of the genus non-red, e. g., *Atax*, *Hygrobates*.

This is a large group and the colours are extremely varied. (These groups are not intended to express the natural relations of the genera.)

The ground-colour of the mites is due to pigment present in the skin. Markings of various sorts are produced by the internal organs showing through the skin.

It is the object of this paper to prove that warning coloration and probably Müllerian mimicry exist among some at least of the Hydrachnidæ.

I am much indebted to Prof. E. B. Poulton for help and encouragement during the preparation of this paper, and to Mr. C. D. Soar for help in identifying the mites, and for other valuable information mentioned later on.

\* Communicated by Professor E. B. POULTON, F.R.S., F.Z.S

## 2. THE MITES OF RAILWAY DITCH, OXFORD.

If there are no particular laws governing the occurrence of colours in mites we should expect to find chance mixtures of colours among the species of any one habitat. In the following example such was clearly not the case. During May 1921 the fauna of a small ditch near Oxford (here referred to as "Railway Ditch") was examined by me. This ditch is connected by several channels with the Thames, but is usually almost stagnant. Only one part of it was studied, an area about 30 yards long and 4 feet wide. Since it is important to know what animals and plants are associated with the mites, a list of the species observed during the course of the work is given below. This list is not by any means exhaustive, but gives some idea of the type of habitat in which the mites were living.

PLANTS: *Ranunculus aquatilis* Agg., *Hottonia palustris* L., *Callitriche aquatica* Sm., *Potamogeton natans* L., *P. perfoliatus* L., *P. densus* L. (*Lemna minor* L., *L. trisulca* L.).

HIRUDINEA: Two large species.

MOLLUSCA: *Limnea stagnalis* L., *L. peregra* Müll., *Planorbis corneus* L., *P. complanatus* L., *P. spirorbis* Müll., *Ancylus lacustris* L., *Bithynia tentaculata* L., *Paludina vivipara* L.

INSECTA:

Coleoptera: *Dytiscus marginalis* L., *Hyphrydus ovatus* L., *Hydroporus palustris* L., *Agabus bipustulatus* L., *Haliplus* sp.

Hemiptera: *Nepa cinerea* L., *Hydrometra stagnorum* L., *Notonecta glauca* L., *Corixa* sp., *Velia* sp., *Gerris* sp.

Neuroptera: Various larvæ.

CRUSTACEA: *Cyclops serratulus* Fischer, *C. prasinus* F. *Chydorus* sp.

*Asellus aquaticus* L.

FISH: *Gasterosteus aculeatus* L.

AMPHIBIA: Frog tadpoles.

The mites and their colours are shown in Table I.

TABLE I.—The Mites of Railway Ditch, May 1921.

SPECIES.	COLOUR.
<i>Hydrarachna globosa</i> De Geer.	Scarlet.
<i>H. schneideri</i> Koen.	Scarlet.
<i>H. distincta</i> Koen.	Scarlet.
<i>H. fuscata</i> Soar.	Dark purple with reddish spot on back.
<i>Eylais hamata</i> Koen.	Scarlet.
<i>Diplodontus despiciens</i> Müll.	Scarlet.
<i>Hydryphantes ruber</i> De Geer.	Scarlet.
<i>Piona longipalpis</i> Krend.	Scarlet with black spots on back.
<i>Limnesia fulgida</i> Koch.	Scarlet with black marks on back.

The ditch was full of breeding 3-spined Sticklebacks (*Gasterosteus aculeatus*). The males were guarding their nests and driving off all intruders fiercely. The mites were not abundant, only about 20 specimens being taken, after a good many days of watching and collecting. This fact made it impossible to do as many experiments as one could have wished. When a scarlet mite did appear, it was extremely conspicuous and sometimes swam near a male fish without being touched.

### 3. THE EVIDENCE FOR WARNING COLORATION.

Experiments were made in May 1921 in order to see whether mites are eaten by Sticklebacks.

*Expt. 1.* A large male 3-spined Stickleback from Railway Ditch was placed in a vessel of water, and starved for three days. It was then offered a *Daphnia pulex*, which it devoured. Directly afterwards a *Limnesia fulgida* was put in. The fish made towards it from an inch or two away, but stopped half or quarter of an inch from it and swerved off. It repeated this after a minute or two. After that the mite was disregarded altogether. When given another and brighter *L. fulgida* the fish went up to it once in the same way, and afterwards ignored it. It was given another *Daphnia* which it devoured eagerly.

*Expt. 2.* The last experiment was repeated on the same fish, *Eylais hamata* being used instead of *Limnesia*. The mite was completely ignored after several inspections.

*Expts. 3, 4, 5.* The same result was obtained when *Diplodontus despiciens*, *Piona longipalpis*, *Hydrarachna distincta*, respectively, were used.

These experiments show that the fish avoided scarlet mites even when it was fairly hungry, that the latter were presumably distasteful to it, and that the fish remembered this fact from its former experience.

*Expt. 6.* A Stickleback was placed in a vessel as before. A *Daphnia* was eaten eagerly. An *Eylais hamata* was put in and avoided by the fish. Another *Daphnia* was eaten. A *Hydrarachna fuscata* was now introduced. The *E. hamata* accidentally bumped into the fish, which whipped round and snapped up the mite, but immediately spat it out again. The fish then approached *H. fuscata* but did not touch it. A *Daphnia* was then put in and eaten.

This experiment shows that *E. hamata* was actually distasteful to the Stickleback, and that *H. fuscata* was avoided.

Mr. Soar tells me that he has never seen any mite eaten except by other mites. He once observed a *Dytiscus* larva which refused to touch a *Diplodontus despiciens*. Piersig [3] quotes an observation of Dugès to the effect that *Nepa* refused to touch water-mites, but does not state what species. Thus, scarlet mites are avoided by two of the fiercest enemies of fresh-water animals, *Dytiscus* and Sticklebacks, both of which were present in



Railway Ditch. [Mites will often attack each other. *Piona longipalpis* was seen to attack *Limnesia fulgida* and *Hydrarachna fuscata*, and Mr. Soar states that *L. fulgida* will often attack *Eylais*.]

*Hydrarachna fuscata*, which is not scarlet, has the peculiar habit of crumpling up its legs and feigning dead when touched. Mr. Soar states that he does not know of any other Water-mite which does this, although mites sometimes are found resting in a crumpled up position. Before we can say what the precise use of this habit is, more experiments are required. But the following occurrence shows that it may be an advantage sometimes.

*Expt. 7.* A *Hydrarachna schneideri* and a *H. fuscata* from Railway Ditch were put in a jar with a specimen of *Agabus bipustulatus* from a pond in Oxford Botanic Gardens in which no mites had ever been seen, although regular collections had been made for nine months. The beetle attacked and ate *H. schneideri*. Meanwhile *H. fuscata* feigned dead during the disturbance and remained unharmed.

This experiment does not prove anything with regard to the distasteful properties of *H. schneideri*, since the beetle was almost certainly unused to scarlet mites.

*Expt. 8.* In the autumn of 1921, a young 3-spined Stickleback from a flood-pond near Railway Ditch was starved for three days and then given a *Tubifex*, which it gobbled up. A *Limnesia fulgida* from Railway Ditch was put in with it. The fish dashed at the mite and caught hold of one leg, but immediately let go and left it. After this the fish went up to within a quarter of an inch of the mite several times, but did not touch it. The mite was left in with the fish for seven days, but still remained uneaten, although the latter had now been starved for ten days.

*Expt. 9.* In the end of February 1922 a young 3-spined Stickleback was taken in Railway Ditch and was starved for four days. (No mites were to be found in the ditch at this time.) A *Simocephalus vetulus* was put in and eaten eagerly. A nymph of *Hydrarachna paludosa* Thon. from a salt stream at Marcham was now put in. This species is coloured very brilliant scarlet. The fish went up to it and took the mite into its mouth, but immediately spat it out. It went up to the mite repeatedly after this without eating it, and followed it round for some time, clearly torn between its ravenous hunger and the unpleasantness of the mite. The latter was now removed.

Two days later, the Stickleback (having now been starved for six days) was given two *Simocephalus*, which it devoured. *H. paludosa* was then introduced. This time the fish snapped up and spat out the mite many times, but sometimes avoided it, and never swallowed it.

This experiment shows among other things the effect of hunger on the reactions of the fish.

All Water-mites possess large skin-glands, provided with so-called "sensory" hairs, whose function has been, so far, uncertain. As Piersig (3) points out, it has long ago been suggested that these glands secrete some unpleasant fluid; but he states that there is not enough evidence to decide whether the mites are distasteful or not. That they are so to Sticklebacks is certain, in view of the experiments here described. The idea that it is the skin-glands which make the unpleasant taste, is supported by the fact that the fish does not injure a mite when it takes it into its mouth, and therefore cannot actually taste its flesh; also by the fact that the mite is spat out so promptly. The anatomy of these glands and the nature of the supposed secretion require to be worked out in detail. The hardness of the body probably helps to render some mites distasteful, as indicated by the fact that a Stickleback when not very hungry will sometimes reject a young *Asellus*, after taking it into its mouth. But this could not apply to such soft-skinned mites as *Eylais* and *Diplodontus*.

These experiments make it clear that Sticklebacks recognize the scarlet mites by their appearance. It is extremely likely that it is the colour which is remembered, although no accurate work has been done on *Gasterosteus*, in order to prove this. But White (8) has recently shown that the American Stickleback (*Eucalia inconstans*) and Mud Minnow (*Umbra limbi*) are well able to distinguish differences in colour as distinct from differences in the intensity of light. She proved by experiment that the fish were capable of associating different colours with their food, though they were unable to distinguish between fine shades of the same colour. The same may well be the case for the 3-spined Stickleback.

There is another point which is of some importance. It may be asked what advantage is gained by mites, seeing that they appear to be uninjured by fish, even after being snapped up and spat out several times. The answer to this is that: (1) Mites must be actually destroyed by some animals before their distastefulness can be realized, e. g. *Agabus*; (2) the fluid which seems to be secreted by the skin-glands would ultimately become exhausted; (3) being continually attacked must interfere with the life processes of the mite. The degree of effectiveness of warning colours depends among other things on the state of hunger of the enemies.

#### 4. THE EVIDENCE FOR MÜLLERIAN MIMICRY.

There is no evidence at present of Batesian mimicry, *i. e.* of edible mimics, among Water-mites. It is unlikely that it exists, in view of the facts that all Water-mites have the large skin-glands and that there are very few cases on record of mites being edible. However, the possibility should not be ignored. There is, on the other hand, strong evidence of Müllerian mimicry

among mites. It seems remarkable that eight species of scarlet mites belonging to six genera occurred in Railway Ditch. Two of these species are members of genera in which the other species are mostly non-red (*Limnesia* and *Piona*). The only species which is not bright red, occurring in the ditch, has a special defensive habit, not found among other mites. The absence of any other non-red species is remarkable, since there is no dispersal difficulty to prevent them from immigrating from the Thames. The shape, size, and mode of swimming of all these species are much the same, except that *Egylais* trails its legs behind.

If we exclude the possibility of coincidence, the explanation might be that the red mites possess some advantage which is not shared by the non-red ones. Now, there may be two important factors affecting the evolution of a group of animals in the direction of having a common colour:—

- (1) In the words of Prof. Poulton, "the feasibility of certain colours and patterns depending upon their effect on the vertebrate eye and thus giving the enemies as easy an education as possible" (4). That is to say, scarlet may have a more striking effect on the retina of the Stickleback's eye than any other colour, and therefore be more effective as a warning.
- (2) Reinforcing this would be the co-operative advantage of Müllerian mimicry as usually understood.

The early stages in the evolution of a set of Müllerian mimics would be easier to conceive of if there was any evidence that the first factor is an important one, and its effect would be greater in the case of animals which, like these scarlet mites, are of one uniform colour and do not possess elaborate patterns. (The latter, where they occur, cannot be explained without the aid of the Müllerian theory.) Therefore, if it can be shown that Sticklebacks remember scarlet mites better than those with other colours, the case in favour of Müllerian mimicry will be correspondingly strengthened. The following experiments show that this may be so:—

*Expt. 10.* The same fish was used as in *Expt. 9*, after being starved for four days. As was seen in that experiment, a scarlet *Hydrarachna paludosa* was refused after one trial. A *Simocephalus* was then put in and eaten at once. A specimen of *Hygrobatas longipalpis* Herm. was introduced. This mite is coloured black and yellow, and is quite conspicuous. The fish snapped it up and immediately spat it out. This it repeated fourteen times at intervals. Another *Simocephalus* was put in and eaten. The mite was again taken in and rejected seven times. Another *Simocephalus* was eaten. The fish now approached the mite four times without touching it. After that the mite was more or less ignored. A *Limnesia undulata* Müll. was now put in. This species is yellow with black or brown spots. The fish took

it in its mouth and spat it out twice, and afterwards avoided it. *Hydrarachna paludosa* (brilliant scarlet) was now introduced, and the fish avoided it after one trial. There were also some *Cypris virens* present, coloured a uniform brownish green. This Ostracod was too hard for the fish to crush and too big to swallow; yet the Stickleback kept rushing at the *Cypris* whenever they moved, trying to swallow them. This it continued to do throughout several days.

This experiment suggests that scarlet was remembered by the Stickleback better than yellow and black, although the hunger of the fish has to be taken into account. But both were more effective than the dull uniform colour of the *Cypris*.

*Expt. 11.* The same fish was used as in *Expt. 1*. It was experienced as regards scarlet mites. A *Daphnia* was eaten eagerly. An *Acercus lutescens* Herm. was put in. This is a small mite, coloured pale pink, dark brown, and yellowish white. The fish snapped up the mite, but immediately spat it out again. This was repeated three times. After this the mite was avoided. A short time afterwards the fish noticed it again, and the whole procedure was repeated (the same number of times). A *Daphnia* was eaten. *Eylais hamata* (scarlet) was introduced, but avoided after inspection. Both mites were removed. Next morning the experiment was repeated. The fish saw *Acercus* and snapped it up, and then spat it out. Next time the mite was avoided. The mite was then removed. Thirty-five minutes later *Acercus* was put in again. The fish went right up to the mite, but did not touch it. After this the mite was ignored. *Daphnia* was put in and eaten. *Eylais* was put in and avoided. This experiment suggests that the fish was able to remember the scarlet much better than the other colours. It is unlikely that the difference in impressions made on the fish was due to the scarlet mite having a more unpleasant taste than the other, since both were spat out equally promptly. It is probable, then, that scarlet is the most efficient warning colour for use in Stickleback-haunted habitats. Perhaps it is only the best for such habitats at one time of year, *i. e.* in the breeding-season of the fish. I observed yellow-and-black mites (unidentified) in a Hampshire pond where 3-spined Sticklebacks occurred on August 4th, 1922. This shows that such mites can exist in some Stickleback ponds. Not much is known about the food reactions of these fish, except that they are usually very fierce and voracious. It is necessary to be very cautious in applying the knowledge about food habits of Sticklebacks in one place to those of another. J. T. Saunders (5) records a pond in which the adult 3-spined Sticklebacks ate nothing but one kind of diatom, while the young ones in the same pond and all the fish of neighbouring ponds were carnivorous. He also states that the fish soon learn to distinguish by sight between different animal foods, and that they are very sensitive to changes in their environment—*e. g.*, the diatom-eaters became carnivorous in captivity. The latter fact might throw some doubt



on the validity of the experiments with mites etc. described here; but the uniformity of the results makes it pretty certain that the fish would reject Water-mites in nature as well as in captivity.

The fact that the fish in Expts. 10 and 11 did not learn well on other colours than scarlet does not weaken the case in favour of warning coloration, since the non-red mites used were not in the presence of their natural enemies. *Acercus lutescens* came from a pond in which there were no fish. *Hygrobates longipalpis* and *Limnesia undulata* were from the Thames. Now, although Sticklebacks are abundant in most rivers, Maxwell (2) says: "It has been observed that the Stickleback is very scarce in the Thames."

The chief importance of these non-red mites here is that it has been shown that they might be at a disadvantage in Stickleback-haunted habitats (where scarlet ones are successful), and that non-red mites actually tend not to come in such places.

Some other evidence may be added to this, though very little is known about the associations of Water-mites.

There is a flood-pond near Railway Ditch which was full of 3-spined Sticklebacks in May 1921 (see Expt. 8). The very large and conspicuous scarlet *Eylais extendens* Müll. was taken here swimming about among the fish. The only other mite was *Piona conglobata* Koch, which is very minute and is inconspicuously coloured. *Hyphrydrus ovatus* was unusually abundant in Railway Ditch in May 1921. This beetle is coloured bright orange below. It secretes a liquid when handled, which smells like honey and may make it distasteful. It is possible that the Müllerian mimicry included this beetle. Shelford (6) records *Limnochares aquatica*, which is a large scarlet mite and is unable to swim, as occurring abundantly in a pioneer association of Chara, in which were also many species of fish. Mr. Soar tells me that all the crawling Water-mites are red, which supports the idea that they are warningly coloured.

## 5. DISCUSSION.

Scarlet is rather rare among animals, except in the tropics. Higgins (1) has suggested that it is due to the fact that red rays are more valuable (there being more energy per unit wave-length than in other colours of light), and are therefore usually absorbed, not reflected. It is more likely that the rareness of scarlet is due to its conspicuousness when seen against natural browns and greens (as in our own road-traffic warning signs). In any case, we generally find that animals are scarlet only when there is some very important use for the colour. For the reason given above, it makes an excellent warning colour. It is possible that red can be seen from further away in water than other colours. This is known to be the case in air.

Any protection gained from warning coloration and Müllerian



mimicry would be, of course, only relative. For instance Piersig quotes Forbes, who found that fish did not entirely refuse to eat Water-mites, and gives as his own observation that *Ranatra* seized and sucked mites without hesitation (3), but does not state whether these were the natural enemies of the mites. Before any generalization can be made about the colours of Water-mites, more information is required about their associations, together with experiments in which their natural enemies are used. Mr. Soar states that many mites vary in colour individually a great deal (e. g. *Piona rufa* Koch). It is quite likely that the colours of other mites than those described here may have some different significance.

In conclusion it may be pointed out that many Land-mites are bright scarlet, and no experiments appear to have been done on them.

## 6. SUMMARY.

1. Ecological observations are described which make probable the existence of warning coloration and Müllerian mimicry among certain species of Hydrachnidæ.

2. Experiments are described which show that these are distasteful to and recognized by Sticklebacks (*Gasterosteus aculeatus*).

3. There is evidence that scarlet is the colour best remembered by these fish. This makes the evolution of such a set of Müllerian mimics more easy to understand.

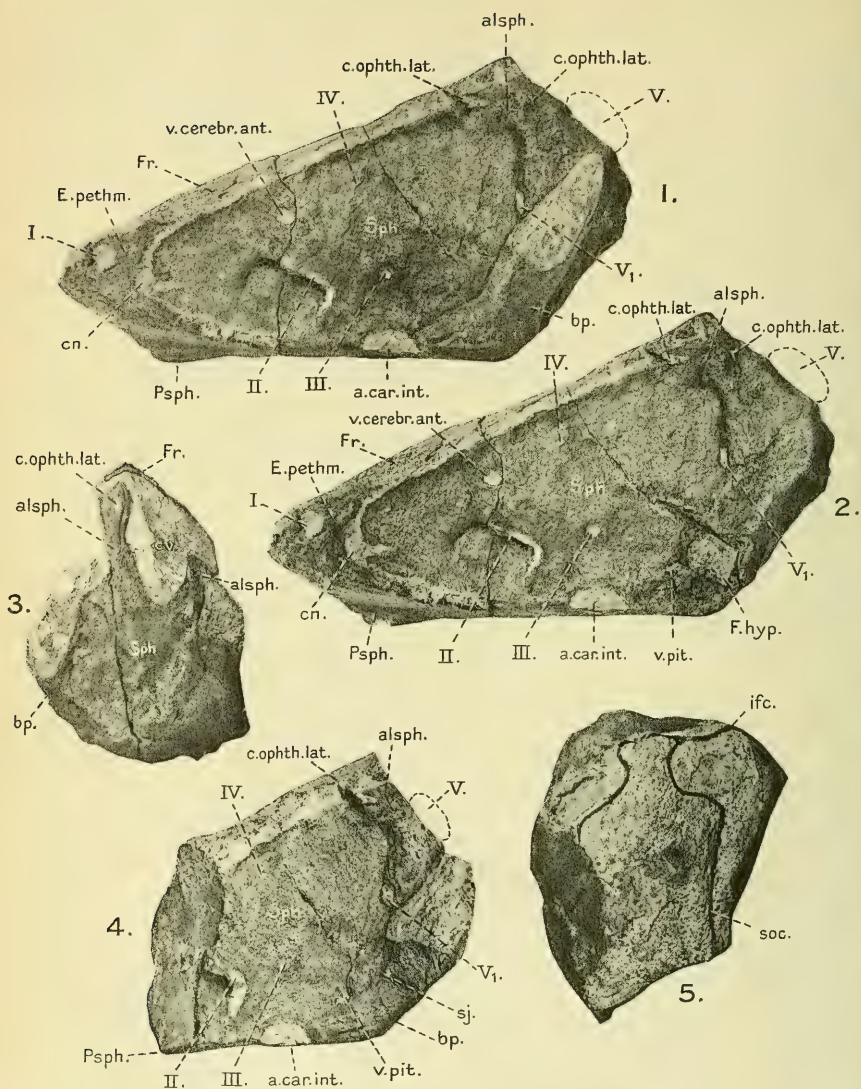
4. Other evidence is given in support of these conclusions.

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DICTYONOSTEUS ARCTICUS and POROLEPIS ? sp.

## 55. Notes on certain Crossopterygians.

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(Plate I.†; Text-figures 1-6.)

## INTRODUCTION.

In the summer of 1921, just as my paper on the Devonian Coelacanthids from Wildungen (Stensiö, 1922 *a*) had been sent to press, there arrived at the Upsala Library an interesting description of *Eusthenopteron*, published by Bryant already in 1919, which accordingly could not be dealt with in my paper just referred to. A few months later there also appeared a very important paper by Watson on the organisation of the Coelacanthids (Watson, 1921). As many of the facts put forward by Bryant and Watson in these papers throw new light on many questions, I have found it of interest to give here some of the views at which I have arrived, partly on the basis of these facts, partly by examining my own material of Crossopterygians. I shall begin with a detailed description of what is known so far of the neurocranium in *Dictyonosteus*, then turning to *Eusthenopteron*, *Porolepis*, and the Coelacanthids.

## DICTYONOSTEUS ARCTICUS Stensiö.

(Pl. I. figs. 1-4.)

The material of this fish to be described below has already been dealt with by me in a preliminary description in 1918 (Stensiö, 1918 *b*), and has further been referred to in my memoirs on the Triassic fishes from Spitzbergen and in my paper on the Coelacanthids from Wildungen (Stensiö, 1921; 1922 *b*, 1922 *a*, pp. 196-198, 204-206). It consists only of an anterior part of the primordial neurocranium with the dermal bones partly preserved. The part is large, measuring 21 cm. in length and indicating that the head of the fish to which it belonged must have attained a very considerable size.

*Primordial Neurocranium.*

The occipital region is totally lacking, as is also the labyrinth region with the exception of a very short anterior part. The remaining two regions, the orbitotemporal and ethmoidal regions respectively, are as a whole rather completely preserved, though partly crushed and broken.

The whole orbitotemporal region and the anterior part of the

\* Communicated by Prof. D. M. S. WATSON, F.R.S., F.Z.S.

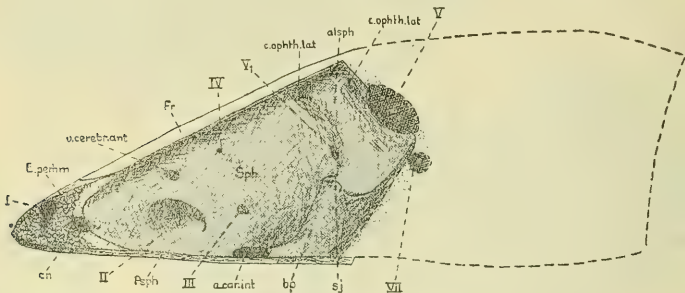
† For explanation of the Plate, see p. 1271.



labyrinth region that is preserved are occupied by an unpaired large bone, the sphenoid (Stensiö, 1921, p. 56), while in the ethmoidal region there is found a paired bone, the exethmoideo-preëthmoid (*cf.* Stensiö, 1922 *a*, pp. 184-185). Both the sphenoid and the exethmoideo-preëthmoid consist chiefly of cancellous bone, and exhibit no centres of ossification nor any radiate structure.

We begin our detailed description with the sphenoid. This bone (*Sph*, text-fig. 1; Pl. I. figs. 1-4) is high at the posterior end, but becomes rapidly lower forward, so that its height at the anterior end is only about a third of that at the posterior one.

Text-figure 1.



*Dictyonosteus arcticus* Stensiö.

Anterior half of the neurocranium in lateral view. The lateral part of the ethmoidal region removed, as are also the lateral parts of the dermal bones of the cranial roof. Cartilage dotted. Somewhat more than a third of the natural size.

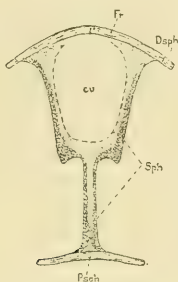
*E.pethm*, exethmoideo-preëthmoid; *Fr*, frontal; *Psp*, parasphenoid; *Sph*, sphenoid; *a.car.int*, canal for the arteria carotis interna; *alsph*, alisphenoid wulst; *bp*, basipterygoid process; *cn*, orbito-nasal canal for vessels to or from or both to and from the nasal fossa; *c.ophth.lat*, canal through the alisphenoid wulst for the n. ophthalmicus lateralis; *sj*, sulcus for the vena jugularis (dorsal end of the sulcus only seen here); *v.cerebr.ant*, canal for the vena cerebialis anterior; *I*, olfactory canal; *II*, opticus canal; *III*, oculomotorius canal; *IV*, trochlearis canal; *V*, trigeminal exit; *V1*, canal for the r. ophthalmicus profundus; *VII*, the probable place of the facialis exit.

The width of the bone taken as a whole is rather small, except at the postero-ventral part where the basipterygoid process (*bp*) is situated. The posterior end of the bone seems to have been separated from the ossification, or the ossification following next behind in the labyrinth region, by a synchondrosis, and that this also has been the case anteriorly towards the exethmoideo-preëthmoid is certain. The former end is in side view angulated in the way shown by text-fig. 1, the latter, on the other hand, convexly arched. The cranial cavity extends forward through the whole length of the bone.

We can distinguish on the sphenoid an unpaired pars basalis, which forms the floor of the cranial cavity, and a paired pars lateralis, issuing upwards from the pars basalis along either of its dorso-lateral edges and extending upwards to the dermal cranial roof, forming the lateral wall of the cranial cavity.

The pars basalis corresponds in its whole extension to about half the height of the sphenoid, its absolute height thus being much longer at the posterior end than at the anterior one. From the anterior end it first diminishes in width backwards, so that some distance anterior to and below the opticus exit (II) it forms only a rather thin wall between the orbits (text-fig. 2). Behind this place it continually grows wider to the posterior

Text-figure 2.

*Dictyonosteus arcticus* Stensiö.

Transversal section through the neurocranium a short distance anterior to the opticus exit. Cartilage dotted. Somewhat more than a third of the natural size.

Fr, frontal; Psp, parasphenoid; Sph, sphenoid; cv, cranial cavity.

end, which is rather broad owing to the large basiptyergoid process (*bp*) on either side. The posterior surface is rather concave (Pl. I. fig. 3), probably in the same way as Watson (1921, p. 335) has found it to be in *Megalichthys* and in the Carboniferous and Permian Coelacanthids. In my description in 1918, when the specimen had not been cleaned from the matrix\*, I came to the incorrect conclusion that this concavity was the fossa hypophyseos and the upper boundary of it the dorsum sellæ (cf. Stensiö, 1918 b, p. 120; pl. iv. fig. 3; pl. v. fig. 1; pl. vi.).

The ventral surface of the pars basalis is straight and plane, and has been situated almost horizontally; the dorsal one, on the other hand, slopes rather much forwards, and is concave from one lateral side to the other—*i.e.*, it is somewhat grooved in a longitudinal direction. At about the middle of its length the

\* The cleaning of the specimen from the matrix has been very difficult, and has taken a long time, as the matrix was a very hard ironstone.

latter surface suddenly deepens to a postero-ventrally directed fossa hypophyseos, which extends nearly to the postero-ventral corner of the pars basalis (*f.hyp*, Pl. I. fig. 2), where it is separated from the synchondrosis behind the sphenoid only by a very thin layer of bone. So far as is known, the fossa hypophyseos does not in any way open on the base of the primordial neurocranium or in the mouth.

On either lateral surface of the pars basalis there is found, as already mentioned, farthest posteriorly the large basiptyergoid process (*bp*). This process partly arises along the ventral, partly along the posterior edge of the lateral surface, and extends rather high upwards, ending dorsally with a truncated end. The process has a dorsal surface represented by a truncated dorsal end, a postero-ventral surface which has been attached to cartilage, a ventro-lateral surface against which the metapterygoid probably articulated, and an antero-dorsal surface which, together with the lateral surface of the pars basalis just anterior to it, forms a rather shallow and indistinct fossa directed with its opening antero-laterally and somewhat dorsally.

In this fossa there opens a wide canal, which perforates the pars basalis in a transverse direction below the fossa hypophyseos to the corresponding fossa on the opposite side. This canal (*v.pit*, Pl. I. figs. 2, 4) communicates with the fossa hypophyseos by a short but wide posteriorly directed branch, and, though it runs ventrally of the posterior part of the fossa hypophyseos, must undoubtedly be the canalis transversus, and have been pierced by the pituitary vein (Allis, 1914; 1919 *a*; *cf.* also Stensiö, 1922 *b*). From its external opening in the fossa described there a very distinct sulcus (*sj*, text-fig. 1; Pl. I. fig. 4) leads upwards to the dorsal end of the basiptyergoid process, a sulcus which must have been developed for the jugular vein (*cf.* Allis, 1919 *a*; Stensiö, 1922 *b*, *loc. cit.*). Accordingly there is no doubt that this vein in its continuation backwards must have run dorsally of the basiptyergoid process.

Immediately in front of the basiptyergoid process of either side there is found close to the ventral edge of the lateral surface of the pars basalis a large oval foramen (*a.car.int*, text-fig. 1; Pl. I. figs. 1, 2, 7) apparently leading into a vertical canal ascending to the cranial cavity. This canal, which must be the canal for the arteria carotis interna, ought to have entered the cranial cavity not far anterior of the fossa hypophyseos, between this and the opticus exit, and thus quite in the normal way (*cf.* Allis, 1897; 1909; 1911 *a*, *b*; 1912 *a*, *b*; 1914; 1919 *a*; Allen, 1905; Danforth, 1912; Stensiö, 1922 *b*).

The partes laterales of the sphenoid (text-figs. 1, 2; Pl. I. figs. 1-4) do not diverge much from one another upwards, thus occupying an almost vertical position. Anteriorly they are rather thin, but they grow slowly thicker backwards. Along their dorsal margins, too, they are partly thin, and so developed as to show that the roof of the primordial neurocranium in the

orbitotemporal region, apart from possible fontanelles, must have been cartilaginous (*cf.* text-fig. 2).

Each of the partes laterales has a somewhat concave posterior edge, which faces postero-dorsally. This edge also is so developed that in part it cannot have been in contact with cartilage, but must have been free, forming the anterior boundary of a great foramen (*v.* text-fig. 1). This foramen must, as comparisons with *Diplocercides* make clear, be the trigeminus foramen, which thus has been situated in the dorsal part of the synchondrosis between the sphenoid and the ossifications in the labyrinth region (*cf.* Stensiö, 1922 *a*).

Along the posterior edge each pars lateralis has on its lateral surface a rather broad but well-marked "wulst," which extends from the upper edge of the pars lateralis downwards and somewhat backwards to the upper end of the basiptyergoid process. This "wulst" (*alsph.* text-fig. 1; Pl. I. figs. 1-4), which I have called the alisphenoid wulst (Stensiö, 1922 *a*, pp. 180, 196-197; 1922 *b*), is perforated close to the dorsal end by a horizontally running canal (*c.ophth.lat.* text-fig. 1; Pl. I. figs. 1-4), which has its posterior opening on the posterior and its anterior opening on the anterior side of the wulst. At the anterior edge of the ventral part of the same wulst, some distance above the basiptyergoid process, there is found the outer opening of a canal (*V<sub>1</sub>*, text-fig. 1; Pl. I. figs. 1-4), leading backward, inward, and somewhat medially to the cranial cavity.

The division of the cranial cavity enclosed in the sphenoid is comparatively narrow throughout its extension (text-figs. 1, 2; Pl. I. fig. 3; *cf.* also Stensiö, 1918 *b*, pl. v. figs. 2, 3). While its height decreases gently forward, its width, on the contrary, seems rather to grow somewhat larger towards the anterior end. Owing to the considerable height of the pars basalis of the sphenoid, the division of the cranial cavity in question, with the exception of the large fossa hypophyseos, is situated totally in the dorsal half of the neurocranium, and it is evident that the division next behind in the anterior half of the labyrinth region also had a similar high position.

From the shape of the division of the cranial cavity just described, we can conclude with great probability that the telencephalon was long and rather high, and that the ventral parts of the diencephalon were strongly developed. Thus the anterior divisions of the brain of the fish must have resembled the corresponding ones in the recent *Ceratodus*, at least with regard to their general shape (*cf.* Bing & Burckhardt, 1905).

The trigeminus branches proper, except the r. ophthalmicus profundus and the lateralis branches accompanying these (or perhaps their roots), have left the cranial cavity through the foramen already referred to, which must be supposed to have existed in the upper part of the synchondrosis between the sphenoid and the bone or bones following next behind in the labyrinth region. The position and probable size of this foramen



are seen in text-fig. 1 (V). After their exit through this foramen, the trigeminus branches proper, accompanied by the n. buccalis lateralis, have evidently passed forward to the orbit laterally of the alisphenoid wulst and dorsally of the basiptyergoid process; while the n. ophthalmicus lateralis immediately took a more dorsal course, entering the canal (*c.ophth.lat.*) in the dorsal part of the alisphenoid wulst and, soon after having left this, reaching the roof of the orbit. As the canal (*c.ophth.lat.*) has a rather small calibre, it seems to me most probable that the r. ophthalmicus superficialis did not pass through it, but ran independently of the n. ophthalmicus lateralis as it does in Sturgeons and certain Siluroids, and as it certainly did also in Saurichthyids (*cf.* Stensiö, 1922 *b*; Workman, 1900, pp. 404-407; Herrick, 1901, pp. 201-203). The r. ophthalmicus profundus trigemini or a somewhat equivalent nerve must apparently have been formed already within the cranial cavity, from where it pierced the pars lateralis of the sphenoid independently of the other trigeminus branches (or their roots) through the canal V, described above (*cf.* Stensiö, 1921, pp. 58-59, 93, 169-170; 1922 *a*, p. 183; 1922 *b*).

The exit of the facialis nerve must, so far as one can judge, have been situated somewhat postero-ventrally of the trigeminus exit, so that the r. palatinus facialis in its way downwards and forwards must have run first posteriorly and then ventrally to the basiptyergoid process before it reached the orbit (*cf.* Allis, 1919 *a*; Stensiö, 1922 *a*).

Of the exit of the n. abducens nothing is known with certainty, but the nerve may perhaps have left the cranial cavity through the trigeminus foramen (*cf.* Stensiö, 1922 *b*).

The olfactory nerve has from the anterior end of the cranial cavity, as we shall see, entered an antero-ventro-laterally running canal in the ethmoidal region.

The opticus has left the cranial cavity far forward. It perforated the pars lateralis of its side somewhat anterior of the middle of the length in a downward and forward direction, and has reached the orbit strikingly low (II, text-fig. 1; Pl. I. figs. 1, 2, 4) immediately dorso-caudally of the thinnest part of the pars basalis of the sphenoid.

Somewhat behind the opticus exit, but only slightly higher than this, is found an oval foramen, which undoubtedly transmitted the n. oculomotorius (III, text-fig. 1; Pl. I. figs. 1, 2, 4).

High up, rather near the cranial roof and approximately midway between the opticus and oculomotorius exits, is found the external opening of a fine canal (IV, text-fig. 1; Pl. I. figs. 1, 2, 4), which must undoubtedly have transmitted the n. trochlearis.

A rather wide canal (*v.cerebr.ant.*, text-fig. 1; Pl. I. figs. 1, 2), which is situated high up anterior of the opticus and trochlearis exits, must probably have been traversed by the vena cerebialis anterior (*cf.* Stensiö, 1921, pp. 168-169) on its way to the orbit.



This canal was considered by me in 1918 as the trochlearis canal (Stensiö, 1918 *b*), a view which must be incorrect in the light of the facts now known.

At the anterior end of the sphenoid, in the suture between this and the exethmoideo-preëthmoid, a rather wide canal (*cu*, text-fig. 1; Pl. I. figs. 1, 2) is found which leads forwards to the olfactorius canal, and which undoubtedly has contained vessels to and from the nasal pit (*cf.* Stensiö, 1922 *b*). Perhaps it may also have been in some relation to the points of origin of the muscoli obliqui of the eye.

The arteria carotis externa must, so far as one can understand, already have been sent out from the arteria carotis communis behind the basiptyergoid process, and has probably run upward approximately as far as to the facialis exit, then turning forward and continuing dorsally of the basiptyergoid process to the orbit. The arteria carotis interna, after its origin behind the basiptyergoid process, must have run forward ventrally to this process and laterally to the parasphenoid to its ascending canal described above in the sphenoid. The position of the ventral opening of the ascending canal in relation to the nerve exits is seen from text-fig. 1 and Pl. I. figs. 1, 2, 4. The vena jugularis, after arriving at the dorsal end of the basiptyergoid process, must have passed backward dorsally of this process, as already pointed out, then continuing backwards between the trigeminus and facialis exits.

There is evidently no trigemino-facialis chamber and no myodome in the fish. According to the course of the nerves and vessels, the basiptyergoid process with its antero-ventral parts undoubtedly corresponds to certain posterior parts of the basiptyergoid process in *Birgeria*, with its dorsal parts on the other hand, corresponding to the basiptyergoid process of the Cœlacanthids (*cf.* Stensiö, 1922 *a*, pp. 205-206; 1922 *b*; *cf.* also pp. 1259-1266 below in the present paper).

The ethmoidal region rapidly decreases in height forwards, becoming very low at the anterior end. It is mainly occupied by the paired exethmoideo-preëthmoid, only certain smaller anterior and dorsal parts being cartilaginous. At the postero-medial part the exethmoideo-preëthmoid is separated from the sphenoid by a short synchondrosis, as already pointed out above. In the posterior two-thirds of the length its plane ventral surface is covered by the parasphenoid. Its lateral surface is accessible for investigation only in the anterior parts, being otherwise concealed by remains of very fractured dermal bones.

As already mentioned, the exethmoideo-preëthmoid is traversed by the rather wide canal for the n. olfactorius (I, text-fig. 1; Pl. I. figs. 1, 2), which runs forwards, downwards, and laterally. The large anterior opening of this canal is incompletely subdivided into a postero-dorsal division situated at the anterior end of the lateral surface of the region and an antero-medial division

situated on the ventral surface of the region, the former of which represents the external, and the latter the internal, nasal aperture. In the present state of preservation, dermal bones form the direct boundary of the external nasal aperture on the dorsal side and of the internal nasal aperture anteriorly, but it is conceivable that in the fresh specimen these walls of the two nasal apertures consisted, at least in part, of cartilage.

The r. maxillaris trigemini and the n. lateralis buccalis ought as usual to have had their course along the ventral edge of the lateral surface of the ethmoidal region, but owing to the imperfect state of preservation of these parts of the region it has not been possible to discover whether a distinct sulcus was developed for them as in several other fishes (Stensiö, 1921, p. 94; 1922 *b*). For the same reason it has not been possible to establish anything with regard to the articulation facet for the anterior end of the palatoquadrate.

From the facts put forward here it is easily seen that the exethmoideo-preëthmoid is so developed that it represents both the exethmoid and preëthmoid (*cf.* Stensiö, 1921, pp. 93-94; 1922 *a*, pp. 184-186).

#### *Dermal Bones of the Primordial Neurocranium.*

The parasphenoid (*Psph*, text-figs. 1, 2; Pl. I. figs. 1, 2, 4; Stensiö, 1918 *b*, pl. v. fig. 1) is imperfectly preserved at both ends. The preserved parts of it cover the whole ventral surface of the sphenoid and the ventral surface of the exethmoideo-preëthmoids in the posterior two-thirds of their length. It thus cannot have extended much farther forward, and it is also conceivable that only a rather small part is lacking at its posterior end. There is no processus ascendens. The centre of ossification is clearly distinguishable, and situated midway between the posterior and anterior ends of the bone. At this place and for some distance forward and behind it the bone is much broader than the ventral surface of the sphenoid, so that it projects here with a free lateral part on either side of this (text-fig. 2).

Just at the centre of ossification a rather fine median, unpaired canal opens on the ventral surface of the parasphenoid. The canal perforates the parasphenoid obliquely upwards and backwards, then continuing backwards between this and the ventral surface of primordial neurocranium towards a place between the ventral openings of the internal carotid canals. The canal ought, so far as one can judge from the conditions in *Amia* (Allis, 1897, pp. 620-621; pl. xxxvi. fig. 61; pl. xxxvii. figs. 62, 63), to have been traversed by the anterior branches of the rami palatini of the facialis nerves, which ought to have accompanied the internal carotid arteries when these entered between the sphenoid and the ventral surface of the primordial neurocranium. Possibly the canal in question for the anterior

branches of the rami palatini also transmitted branches from the internal carotids.

If we imagine that a processus ascendens homologous with that in the Teleosts (*cf.* Stensiö, 1922 *b*) was developed on the parasphenoid of *Dictyonosteus*, this process ought to have issued from the stretch of the bone situated between the hind end and the anterior border of the internal carotid canal and the arteria carotis interna, and the n. palatinus facialis would thus have come to run medially of it between it and the ventro-lateral parts of the basipterygoid process.

Of the vomer nothing is preserved in the specimen.

The arrangement and shape of the different bones in the part preserved of the dermal cranial roof is seen in text-fig. 3. The bones were described by me in 1918, and especially later in connection with my account of the Coelacanthids from the Triassic of Spitzbergen, and I have here nothing of interest to add to these descriptions (Stensiö, 1918 *b*, pp. 116–118; 1921, pp. 133–134).

In the present state of preservation of the fish the external nasal aperture is bounded directly on the dorsal side by the two anterior nasal elements and a rostral, while the external boundary of the internal nasal aperture is probably formed by the premaxillary and the rostral elements behind this.

#### *Sensory Canals of the Head.*

The infraorbital canal anastomoses on the snout with its fellow of the opposite side in a well-developed ethmoidal commissure, which is situated in the rostral elements. The supraorbital canal traverses the dermosphenotic, the lateral part of the frontal, and the three nasal elements, from the anterior one of which it enters the rostral plate situated next to the median line, there anastomosing with the infraorbital canal. The exact course of the supraorbital canal is clearly seen in text-fig. 3.

Of the number of sensory canal organs and tubuli nothing is known so far.

As we shall see from the subsequent description, the sensory canals on the snout in *Porolepsis* run exactly like those in *Dictyonosteus*.

#### EUSTHENOPTERON FORDI Whiteaves.

The material of this fish at my disposal consists of two small specimens collected by Professor P. D. Quensel, Stockholm, during his journey to Canada in 1913, and which were kindly presented to the Palæontological Institution at Upsala.

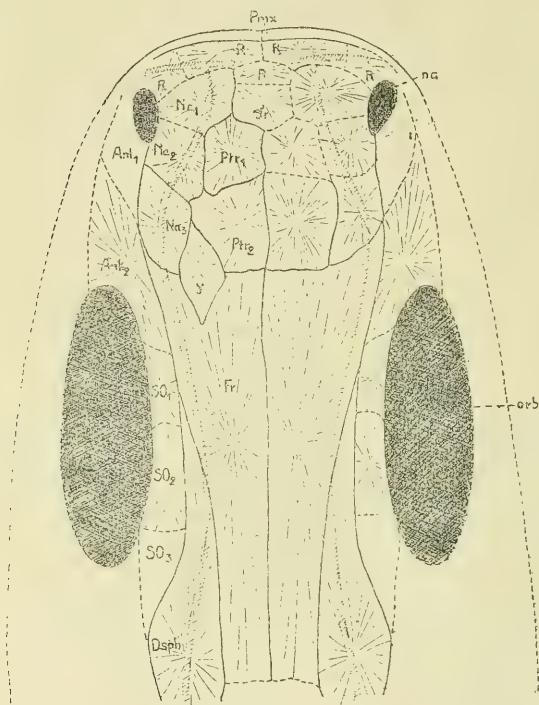
The two specimens are well preserved with regard to the dermal bones, but exhibit on the other hand hardly anything of the primordial neurocranium. My account of this below is therefore based exclusively on the description published by Bryant 1919 on the material in the Buffalo Museum.

*Primordial Neurocranium.*

The general shape of the primordial neurocranium is almost as in *Diplocercides* (Stensiö, 1922 a). The degree of ossification is, however, evidently much less than in this.

The basioccipital and the paired lateral occipital described by Bryant are both rather thin, and it seems very probable, under

Text-figure 3.

*Dictyonosteus arcticus* Stensiö.

The anterior part of the cranial roof. Sensory canals with dotted lines and shading. From P. 355. 1/2.

*Ant*<sub>1</sub>, anterior antorbital element; *Ant*<sub>2</sub>, posterior antorbital element; *Dsph*, dermosphenotic (dermal postfrontal); *Fr*, frontal; *Ir*, interrostral; *Na*<sub>1</sub>-*Na*<sub>3</sub>, nasal elements; *Pmx*, premaxillary; *Ptr*<sub>1</sub>, anterior postrostral element; *Ptr*<sub>2</sub>, posterior postrostral element; *R*, rostrals; *So*, supraorbitals; *na*, external nasal aperture; *orb*, orbita; *y*, accessory bone-plate.

the presumption that Bryant's text-fig. 56 is correct, that they did not directly bound either the chorda, which certainly extended into the basis cranii for some distance, or the cranial



cavity, but that the medial parts of the lateral and ventral walls of the occipital region consisted of cartilage. Expressed in another way: the ossification in the occipital region probably occupied only the external parts of the region, while the inner ones were cartilaginous. The basioccipital has a rather considerable extension forward, and actually lies with more than its anterior half in the labyrinth region. There cannot, however, be any doubt of its homology. The lateral occipital is strikingly high, extending from the basioccipital below nearly to the dermal cranial roof dorsally (Bryant, 1919, text-fig. 3), thus partly occupying the position of the supraoccipital, which according to Bryant is totally lacking. The lateral occipital is said by Bryant to be perforated by a fine canal, but as he does not describe the course of this canal, one cannot decide with full certainty whether it is a canal for a dorsal branch from the n. lineæ lateralis or the vagus canal, although the latter alternative seems to be the more probable one. If however, the canal should reveal itself to have transmitted a dorsal branch of the n. lineæ lateralis, the vagus nerve must have perforated the lateral wall of the primordial neurocranium immediately anterior of the lateral occipital.

In either lateral wall of the labyrinth region of the fish, Bryant, 1919, p. 18, describes five ossifications. One of these ossifications he calls the pro-otic, another the opisthotic. The three remaining ones he considers it impossible to identify, and accordingly he does not name them.

The description which Bryant gives of the pro-otic is not sufficient to make fully clear the shape and actual extension of the bone. As I understand his account, the pro-otic is a rather low bone (*cf.* his text-fig. 5 *a* and pl. ix. fig. 3), which does not by far extend to the cranial roof dorsally. It is perforated by a canal, one of the openings of which is situated approximately at the middle of the length of the bone just at the boundary between its ventral and lateral surfaces or perhaps on the ventral surface, though close to the lateral edge (*cf.* Bryant, 1919, text-fig. 4; pl. ix. fig. 3; pl. xiv. figs. 4, 5). The canal is considered by Bryant to have transmitted the n. facialis (he evidently means the truncus hyoideo-mandibularis of this nerve), but he gives no statements either as to its course nor as to the position of its other opening, and the facts so far known do not seem to support this view. As far as can be judged from the conditions in recent fishes, the canal seems most probably to have been developed for the carotis externa on its way upwards from the cranial basis to approximately the height of the trigeminus and facialis exits (*cf.* Allis, 1897, pp. 497-500; 1908, pp. 219-221; 1909, pp. 51-53, 185-187; 1911 *a*, pp. 284-287; 1914; 1919 *a*; Allen, 1905, pp. 51-56; Danforth, 1912, pp. 435-442; Stensiö, 1922). The truncus hyoideo-mandibularis ought not to have run so strongly downwards that it can be thought to have pierced the canal.



The exact position of the pro-otic of Bryant's description in relation to the sphenoid is not clear, but it seems to me very probable that its anterior end in the fresh specimens ought to have been situated much more ventrally than it has been drawn in his text-fig. 5, and at the same time also closer to the sphenoid than in this text-fig. The bone actually seems to me to correspond only to the basal parts of the corpus of the prootico-opisthotic in post-Devonian *Cœlacanthids* (cf. Stensiö, 1921, pp. 55, 120-121; 1922 *a*, pp. 199-201).

The "small quadrangular bone," which according to Bryant is attached by suture to the outer and hinder margins of the pro-otic and which extends nearly vertically upward to the cranial roof (Bryant, 1919, p. 18), must evidently correspond to some dorsal part of the corpus of the prootico-opisthotic in the post-Devonian *Cœlacanthids*. The description and the figures given by Bryant have failed to convince me that the bone is independent, and I cannot help suspecting that in reality it may be simply a broken dorsal part of the pro-otic.

The bone which Bryant interprets as the opisthotic, much resembles, as he points out (p. 18), the opisthotic in certain *Stegocephalians*, and undoubtedly represents an opisthotic to some extent.

The two remaining bones of the region, which are both small, are imperfectly known, and it is not possible to decide whether they are broken parts of the other bones or not.

In the anterior half of the bottom of the labyrinth region there is in the present state of preservation a large opening bounded by the basioccipital behind, by the sphenoid anteriorly, and by the pro-otics laterally. This opening, which occurs also in *Cœlacanthids* (Stensiö, 1921, pp. 58, 121; 1922 *a*, pp. 173, 202), apparently must have existed in *Dictyonosteus* too. It is situated entirely behind the hypophysis, was probably traversed by the anterior end of the chorda, and corresponds fairly well in its position to the fenestra basicranialis posterior in the embryos of reptiles (Gaupp, 1905, pp. 663, 757-760, figs. 382, 383; Allis, 1919 *c*; Stensiö, 1922 *a*, p. 202). In the fresh specimens it was probably at least to a great extent filled by cartilage.

That it cannot be the fossa hypophyseos, as Bryant presumably means (pp. 18-19), is fully evident from the conditions in *Dictyonosteus* and the *Cœlacanthids*.

The orbitotemporal region and the antero-ventral end of the labyrinth region are occupied by a large unpaired bone, the sphenoid, which is on the whole very similar to that in *Dictyonosteus* (cf. pp. 2-9 above). Thus its general shape is as in the latter fish, and it has a paired basiptyergoid process and a paired alisphenoid wulst situated in the same way as in this fish (cf. Bryant, 1919, text-fig. 5 and pl. ix. figs. 2, 3), and the division of the cranial cavity enclosed in it as well as several of the canals piercing it are in the main as in this. On the other hand, if Bryant's account is correct, it

extends, contrary to that in *Dictyonosteus*, far forward in the ethmoidal region, thus probably including in its anterior parts the homologues of the exethmoideo-preëthmoids (*cf.* pp. 9-10 above). Bryant's account of the anterior parts of the bone is, however, very incomplete, and as in addition the figures he publishes are not very distinct and lack letters of reference, it is impossible to understand how the conditions actually are there.

In accordance with the conditions in *Dictyonosteus* and *Diplocercides* the n. trigeminus must have pierced the cartilaginous part of the cranial wall just behind the dorsal half of the sphenoid. The exit of the n. facialis has probably been situated somewhat more postero-ventrally, though also in the cartilaginous part of the cranial wall behind the sphenoid (*cf.* Stensiö, 1922 *a*).

If my opinion, just given, with regard to the position of the trigeminus and facialis is correct, it follows from this that the small cartilage bone that is seen in Bryant's text-fig. 5 immediately beneath the dermal cranial roof some distance behind the sphenoid would be homologous with a dorsal part of the process lettered *f*<sub>1</sub> by me in the post-Devonian *Cœlacanthids* (Stensiö, 1921), and the corresponding antero-dorsal part on either side of the compound occipito-labyrinth ossification in *Diplocercides*. This small cartilage bone is, however, so far as I can find, not mentioned by Bryant in his description.

The upper part of the alisphenoid wulst is pierced by a horizontal canal for the n. ophthalmicus lateralis, exactly as in *Dictyonosteus*. The anterior opening of this canal is seen in Bryant's text-fig. 5 and also, though less distinct, in his pl. ix. fig. 3. The presence of this canal is undoubtedly a strong support for my view, given above, as to the position of the exits of the n. trigeminus and the n. facialis.

The canal which is stated by Bryant to open in a recess on the external surface of the sphenoid just anterior of the basipterygoid process, must evidently have transmitted the pituitary vein. According to Bryant it leads forwards to a "chamber" on the posterior basal part of the sphenoid—a "chamber" which is said to be open behind and which, with some doubt, is taken to be the anterior end of a myodome. That the "chamber," which in another place is termed by him a "pocket," cannot be a part of a myodome is evident, and it is quite certain that no posterior myodome was developed, but that the conditions were as in *Dictyonosteus* in this respect. If the statements given by Bryant were correct, the "chamber" in question would therefore be the ventral part of the fossa hypophyseos. As, however, as far as can be judged, it is very wide, I feel inclined to think that Bryant may have made a similar mistake as I did in 1918 when describing the corresponding part of the sphenoid in *Dictyonosteus* (*cf.* p. 1242 above). I thus rather fear that in the "chamber" we are

concerned simply with the concavity filled with stone in the posterior end of the pars basalis of the sphenoid, and that the canal for the pituitary vein actually does not open there, but runs somewhat in front of it, ventrally of the fossa hypophyseos, exactly as it does in *Dictyonosteus*.

The foramen seen in Bryant's figures some distance in front of the upper end of the basiptyergoid process at about the middle of the height of the sphenoid corresponds approximately to the external opening of the oculomotorius canal in *Dictyonosteus*, but a certain interpretation of it is not possible, as we do not know the course of the canal leading medially from it, nor several of the other canals of the region. It actually seems to have a position somewhat too far anteriorly to be the external opening of the canal for the ramus ophthalmicus profundus trigemini and, on the other hand, too far back to be the external opening of the opticus canal.

The foramen which in Bryant's figures is seen in the anterior part of the sphenoid may probably be the external opening of the opticus canal. This interpretation is specially supported by the fact that the eye has been situated far forward.

No other foramina or canals that can be thought to have transmitted the n. trochlearis, the r. ophthalmicus profundus trigemini, the arteria carotis interna, and the v. cerebialis anterior are described by Bryant, nor are any canals of this sort clearly discernible in the figures he gives of the different specimens, though they must of course exist.

As is evident from the facts given here, the vena jugularis, the r. palatinus facialis, and the internal carotid artery must in relation to the basiptyergoid process have had the same course as in *Dictyonosteus*.

Of the primordial skeleton of the ethmoidal region of the fish there is nothing to be added to what has already been written above (p. 1253).

#### *Dermal Bones of the Primordial Neurocranium.*

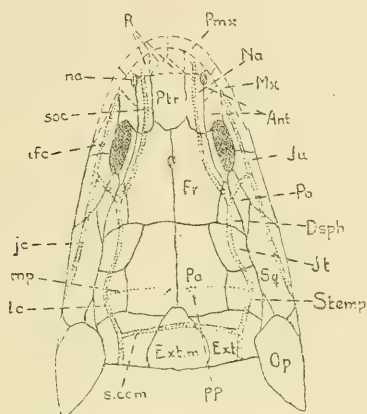
The parasphenoid is, according to Bryant's description, developed in the same way as that in *Dictyonosteus* and *Sauripterus* (cf. Eastman, 1917, pl. vii. fig. 5), but is much more narrow than in these two forms. In my specimens there are only fragments of it preserved. It is noteworthy that it seems to be very firmly connected with the sphenoid. The paired vomer seems to show the normal conditions. Nothing of it is seen in my specimens.

If, after these short remarks on the bones of the ventral surface of the primordial neurocranium, we turn to those of the dorsal one (text-fig. 4), it is clear at once that Bryant has correctly recognized the extrascapular bones, the parietal, the supratemporal and the intertemporal, and it ought also to be added here that the sutures between the extrascapular bones

mutually and between these and the bones in front are more correct in Bryant's text-fig. 2*a* than in the restoration published by me in 1921 (Stensiö, 1921, text-fig. 57)\*.

Between the anterior end of the intertemporal and the postero-lateral corner of the frontal there is in my specimens a very distinct small dermosphenotic (*Dsph*, text-fig. 4), and I also find from pl. v. fig. 2 and pl. iii. fig. 2 in Bryant's paper that the

Text-figure 4.



*Eusthenopteron fordii* Whiteaves.

Dermal cranial roof. After a specimen belonging to the Palaeontological Institution, Upsala. The sensory canals marked with dotted contours and shading. 1/1.

*Ant*, antorbital; *Dsph*, dermosphenotic; *Ext*, lateral extrascapular; *Ext.m*, median extrascapular; *Fr*, frontal; *It*, intertemporal; *La*, lacrymal; *Mx*, maxillary; *Na*, nasal; *Pa*, parietal; *Pmx*, premaxillary; *Ptr*, postrostral; *R*, rostrals and interrostrals; *So*, supraorbital; *Stemp*, supratemporal; *ifc*, infraorbital sensory canal; *lc*, cephalic portion of the main lateral line; *mp*, groove indicating the position of the middle head line of pit organs; *na*, external nasal aperture; *orb*, orbital entrance; *pp*, groove indicating the position of the posterior head line of pit organs; *soc*, supraorbital sensory canal.

same bone was an independent element in the specimens investigated by him. Its exact position and relation to the sensory canals is shown in text-fig. 4 and in my restoration published in 1921 (Stensiö, 1921, text-fig. 57), and will be further dealt with below in the account of the sensory canal system.

The frontal in Bryant's restorations thus has a too large extension postero-laterally. The pineal foramen between the two frontals is not distinct in my specimens, though I can

\* This was due to the fact that my restoration was made after a specimen showing the inner surfaces of the bones.



conclude with the guidance of Bryant's figures where it must have been situated.

The bone which is held by Bryant to be the postfrontal is clearly seen to consist of two independent bones in both my specimens (text-fig. 4), and I also find there that the posterior one of these two bones, which is undoubtedly a compound supraorbital (*so*), extends so far backwards as to meet the anterior end of the dermosphenotic. The anterior bone (*Ant*), on the other hand, is situated mainly anterior of the orbit, forming the anterior boundary of the entrance to this, and is certainly to be interpreted as an antorbital bone. In the main, the supraorbital and the antorbital are correctly drawn in my restoration published in 1921 (Stensiö, 1921, text-fig. 57; the suture line between the nasal and antorbital has fallen away on the left side of this figure).

The postrostral elements of the fish have fused to a rather large unpaired plate (*Ptr*, text-fig. 4), as described by Bryant (called by him interfrontal), and my restoration in 1921 (text-fig. 57), is thus incorrect in this respect.

The paired nasal bone is well seen in one of my specimens. It is situated along the lateral edge of the postrostral plate, extending forwards to the anterior end of this plate, backwards on the other hand somewhat farther (*Na*, text-fig. 4). Its length thus exceeds that of the postrostral plate. The breadth is rather small, and constitutes only about one-half of the length. Throughout its length the bone is pierced by the supraorbital sensory canal. My restoration in 1921 thus showed correctly its approximate shape and relations. It is also noteworthy in this connection that the left nasal bone of the specimen actually seems to consist of two or three independent elements, the conditions thus much resembling those in *Dictyonosteus*.

That the shape and extension of the nasal bone in Bryant's restoration (his text-fig. 2*a*) must be incorrect is thus evident. That this is the case is also seen from pl. iii. fig. 2 in Bryant's paper in question, where the bone is rather well displayed in ventral aspect and shows a longitudinal rounded ridge caused by the sensory canal in it.

Anterior to the postorbital plate and the nasals, I find in the smallest of my specimens (the one that has the nasals well displayed) fragments of a transverse series of bone-plates, which are the rostrals and probably also the interrostrals, and finally anterior to these the rather narrow premaxillaries. The number of the rostrals and interrostrals cannot be ascertained, and it is also impossible to make out anything as to the exact shape either of any of these bones or of the premaxillaries. A rostral plate is also observed by Bryant (p. 9). That he has not seen more of these plates is easy to explain, as they are very difficult to observe and in larger specimens have perhaps fused more or less intimately with the premaxillaries or other neighbouring bones.



*Dermal Bones of the Cheek.*

The dermal bones of the cheek posterior of the orbital entrance seem in the main to be correctly described by Bryant. In my specimens I can clearly observe the postorbital, the jugal, the squamosal, and the preopercular element. The jugal ought, perhaps, to have a larger extension forward beneath the orbital entrance than Bryant has given it in his restoration (his text-fig. 2).

*Visceral Skeleton.*

The visceral skeleton is badly preserved in my specimens, but I find, however, that Bryant is correct in distinguishing a dermo-palatine (termed palatine by him), an ectopterygoid, and an entopterygoid.

*The Sensory Canals of the Head.*

The sensory canals proper form closed canals in the bones, and open outwards with tubuli in the normal way. As the bones are usually thickened on the inner side along the sensory canals, the course of these canals can be rather well traced without preparation in those cases where the bones display their inner surfaces. This is partly finely shown by certain of Bryant's figures, *e. g.* pl. iii. fig. 2; pl. v. figs. 2, 3. At least most of the structures described by Bryant as sensory canals proper are grooves indicating the position of lines of pit organs, as we shall see from the subsequent account.

The supraorbital canal (*soc*, text-fig. 4) is very well preserved in my specimen nearly throughout its length. Its posterior end is situated in the dermosphenotic, where it anastomoses with the infraorbital canal. From there it runs forward through the lateral part of the frontal, and then pierces the nasal in a longitudinal direction. From the nasal it must have entered one of the lateral rostral plates, in which it probably anastomosed with the infraorbital canal of its side. The sensory organs in it have, as far as one can judge, been comparatively few, as the foramina for nerve-branches through its lower wall are comparatively few (*cf.* Allis, 1889, pl. xlii.; Cole, 1898, pl. xxii.; Herrick, 1899, pl. xvii.; 1901, pl. xiv., etc.).

The infraorbital canal [*ifc*, text-fig. 4]: defined as in my memoir on the Triassic fishes from Spitzbergen; Stensiö, 1921, p. 103] has its posterior end at the boundary between the supratemporal and intertemporal. In its course forward it pierces first the intertemporal, then enters the dermosphenotic, in which it anastomoses with the posterior end of the supraorbital canal, as mentioned in the description of this region. Just at this anastomosis it turns laterally, and continues laterally and downwards on the cheek, where it pierces the postorbital, the jugal, and certainly also the lacrymal. It probably was in communication with its fellow of the opposite side through an ethmoidal

commissure, and it is also conceivable that its anterior parts anastomosed with the anterior end of the supraorbital canal as pointed out above, but it is not distinctly preserved anterior of the orbit in my specimens.

In the jugal there issues from the infraorbital canal a jugal canal (*jw*, text-fig. 4), which runs backwards and downwards to the squamosal, in which it continues to the postero-ventral corner. In its further course this canal must have entered the quadratojugal, if the restoration of this bone given by Bryant is correct. As the most postero-ventral part of the canal seems to be homologous with a ventral part of the preopercular canal (*cf.* Stensiö, 1921, pp. 76-77), the quadratojugal ought to comprise a preopercular component (*cf.* Pearson, 1922, pp. 56-58).

A true preopercular canal is not developed. The mandibular canal is not clearly seen in any specimens.

The cephalic portion of the main lateral line (*lc*, text-fig. 4) has its anterior end at the boundary between the supratemporal and intertemporal, where it is directly continuous with the posterior end of the infraorbital canal. It runs backward through the supratemporal and the lateral one of the three extrascapular bones. Through a well-developed supratemporal commissure (*s.com.*, text-fig. 4), which pierces the three extrascapular bones transversely, it is in communication with that of the opposite side.

On the posterior part of the dorsal surface of the frontal there is found a transverse fine groove (*mp*, text-fig. 4), which continues laterally also over an adjacent part of the supratemporal. Another groove (*pp*, text-fig. 4), which, however, is very short, issues from the medial end of the former in a postero-lateral direction. The two grooves which are described by Bryant as a sensory canal proper (p. 12) and which, as it seems, have been interpreted in this way also by Watson (1921, p. 334), are undoubtedly developed for lines of pit organs. The longer of them probably lodges the middle head line of these organs, and the short obliquely running one the posterior head line (*cf.* Stensiö, 1921, pp. 218, 263; 1922 *a*, pp. 224, 235; 1922 *b*: *cf.* also Allis, 1899, pp. 502-509; 1900, p. 445; 1903, p. 187; 1905, pp. 406, 410, 418, 440, 452, 465, 469, 474, 484; Herrick, 1901, pp. 222-223, pl. xiv.: Pander, 1860, taf. iii. figs. 1, 3, 4, 12, 13, 23; taf. iv. fig. 2; Jaekel, 1911, figs. 84, 85). I find no certain traces of any anterior head line.

Of the other structures described as sensory canals by Bryant, the posterior one of the two on the mandibula is clearly shown in my specimen to be a pit line, and the same ought also to be the case with the other ones shown in his restorations (Bryant's text-figs. 2 *c*, 3 *b*).

As is evident from this description, the sensory canals proper of *Eusthenopteron* are developed exactly as described by Goodrich in *Osteolepis* (Goodrich, 1919) and by me in *Dictyonosteus* and

the Coelacanthids (Stensiö, 1921). The pit lines seem, so far as is known, to agree rather well with those in other Crossopterygians.

*POROLEPIS?* sp.

Among the material collected by the Norwegian expeditions in the Lower Devonian strata of Northern Spitzbergen, and for the investigation of which I am indebted to Professor J. Kiaer, of Kristiania, there is an anterior part of the cranial roof, which in this connection deserves some remarks. The part has belonged to a very large fish, probably referable to the same genus as the scales known under the name *Porolepis posnaniensis* Kade (cf. Woodward, 1891, p. 9; Stensiö, 1918 a, pp. 66-73).

On the upper surface of the part present (Pl. I. fig. 5) no sutures at all can be observed. If, however, the outer layers of the bones are removed, the radiation from their ossificatory centres appears, though not so distinctly as in *Dictyonosteus* or *Eusthenopteron* owing to the less favourable state of preservation of the bone tissue. By means of this method, I have been able to observe that the division of the dermal roof covering the ethmoidal region consists of a large number of plates, probably even larger than in *Dictyonosteus*. The exact arrangement and extension of these plates as well as their number can, however, not be made out with the help of the fragmentary material at my disposal. One can only see clearly that the nasal is represented by two or three plates. The supraorbital sensory canal (*soc*, Pl. I. fig. 5) runs exactly as in *Dictyonosteus*. It communicates anteriorly with the anterior parts of the infraorbital canal (*ife*) of its side, which in its turn anastomoses with that of the opposite side through a well-developed ethmoidal commissure (*ethm.com.*), the conditions thus being also in these respects as in *Dictyonosteus*.

THE COELACANTHIDS.

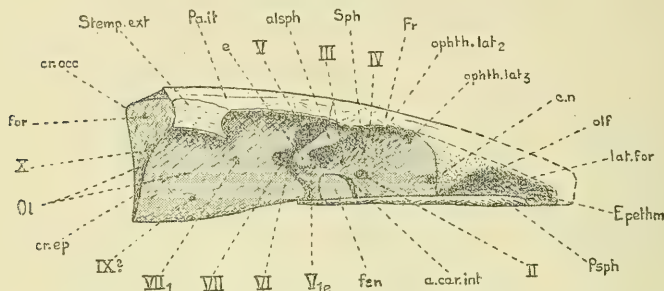
The Coelacanthids are now rather completely known (Stensiö, 1921, 1922 a, 1922 b; Watson, 1921), and I have here only certain remarks to make on them.

It is easily seen that the sphenoid of *Diplocercides* agrees well with that of the Rhipidistids in most features, and there can be no doubt that the soft anatomy of the region occupied by this bone in *Diplocercides* in the main must also have shown great agreement with that of the corresponding region in the Rhipidistids.

In *Diplocercides* (text-fig. 5) we can clearly see that the trigeminus branches proper or their roots, with the exception of the r. ophthalmicus profundus, which has its exit more forward, have pierced the cranial wall just postero-dorsally of the basipterygoid process and at the hinder border of the alisphenoid wulst, together with the r. ophthalmicus lateralis and n. buccalis lateralis (or their roots). From this place all these nerves have

evidently run forward dorsally of the basiptyergoid process. One of them, the n. ophthalmicus lateralis, has pierced the dorsal part of the alisphenoid wulst through an anteriorly running canal, perhaps accompanied by the r. ophthalmicus superficialis trigemini, while the other ones certainly had their passage more ventrally on the lateral side of the alisphenoid wulst. From the conditions in *Dictyonosteus* one can conclude with rather great probability that in *Diplocercides* the vena jugularis also ought to have passed dorsally of the basiptyergoid process.

Text-figure 5.

*Diplocercides kayseri* (V. Koenen).

Neurocranium from the right side. Cartilage dotted, cartilage bones shaded. 2/1,  
From Stensiö, 1922 (1922 a).

*E. pethm*, exethmoideo-preëthmoid; *Fr*, frontal part of the dermal cranial roof; *Ol*, occipito-labyrinth ossification; *Pa.it*, parieto-intertemporal; *Psph*, parasphenoid; *Sph*, sphenoid; *Stemp.ext*, supratemporo-extrascapular; *a.car.int*, ventral opening of the unpaired canal for the internal carotid; *alsph*, alisphenoid wulst; *c.n*, canal for vessels to or from the nasal fossa (probably a vein canal); *cr.ep*, epiotic crista; *cr.oc*, occipital crista; *e*, basiptyergoid process; *fen*, anterior division of the myodome; *for*, canal probably for a dorsally bounded branch from the n. lineæ lateralis; *lat.for*, foramen probably for the anterior branches of the r. maxillaris trigemini and n. buccalis lateralis; *olf*, exit of the olfactory nerve in the nasal fossa; *ophth.lat2*, anterior opening of the canal through the alisphenoid wulst for the n. ophthalmicus lateralis; *ophth.lat3*, posterior opening of an anterior canal for the n. ophthalmicus lateralis; *II*, optic canal; *III*, oculomotorius canal; *IV*, trochlearis canal; *V1e*, canal for the r. ophthalmicus profundus trigemini; *VII*, facialis canal; *VI*, probably the canal for the r. palatinus facialis or perhaps the canal for the abducens; *IX?*, presumed position of the glosso-pharyngeus exit; *X*, canal for the n. vagus, n. lineæ lateralis, and v. encephalica posterior.

In *Axelia* we have a form which with regard to the position of the basiptyergoid process agrees rather well with *Diplocercides* (Stensiö, 1921, text-figs. 39, 40). Moreover, we have there a long well-developed homologue to the alisphenoid wulst of *Diplocercides*, and on the lateral surface of this homologue, which



forms a postero-ventral process from the fronto-dermosphenotic, there runs an antero-caudal sulcus, which certainly corresponds to the canal for the n. ophthalmicus lateralis in *Diplocercides*. These facts and the conditions in general in *Axelia* show that the trigeminus branches (with the exception of the r. ophthalmicus profundus), the lateralis nerves accompanying them, and the vena jugularis ought all to have run dorsally of the basiptyergoid process as in *Diplocercides* and the Rhipidistids.

The basiptyergoid process in *Winania* and *Macropoma*, though situated very high up, issues, however, just at the basis of the obvious homologue of the alisphenoid wulst and just below the level of the floor of the cranial cavity. It actually has the same position as in *Diplocercides* and *Axelia*, but the cranial basis below it has grown much deeper in these. There is thus no reason to believe that in *Winania* and *Macropoma* the trigeminus branches, the lateralis branches accompanying these, and the v. jugularis would have run in another way in relation to the basiptyergoid process than in *Axelia*, *Diplocercides*, and the Rhipidistids.

Consequently the view put forward by Allis in a recent paper (1922, pp. 149-152) that the vena jugularis, the trigeminus branches, and the lateralis nerves accompanying these passed ventrally of the process termed the basiptyergoid process by me seems untenable, as far as we can judge at present. It is absolutely certain that the basiptyergoid process of my descriptions of the Coelacanthids cannot be a postorbital process as Allis concludes. A single glance at the conditions in *Diplocercides* and *Axelia* is sufficient to show the impossibility of this view.

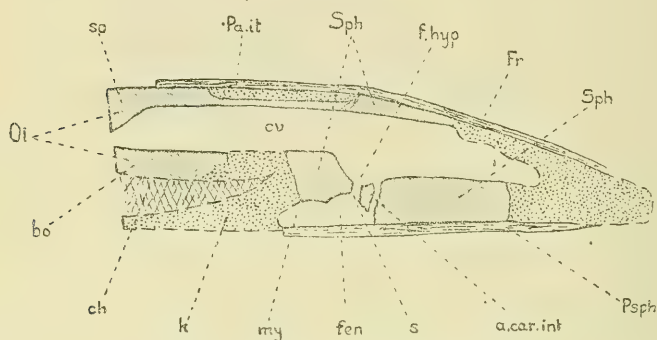
In his argument against my view of the basiptyergoid process in the Coelacanthids, Allis also says that as the hyomandibula in these fishes is evidently of the teleostome type, the jugular vein must have passed internal to it (Allis, 1922, p. 151; 1915), and that this vein accordingly cannot have run so high up as I have maintained, *i. e.* it cannot have run dorsally of the basiptyergoid process. He evidently bases his account (*cf.* Allis, 1922, pp. 150, 151) in this point on Reis's description, having probably overlooked my statements (Stensiö, 1921, pp. 114, 118-119) that the dorsal part corresponding to the hyomandibula of the hyoid arch in the Coelacanthids is reduced, and that the hyomandibula of Reis's description is simply a part of some of the ossifications in the primordial neurocranium. The epihyal, which in the fossil state of the Coelacanthids forms the dorsal part of the hyoid arch, has been attached to the primordial neurocranium only with ligaments. How far dorsally these ligaments extended it is impossible to say, but it seems to me most probable that they were rather short, and that the vena jugularis passed totally dorsally of them and thus dorsally of the hyoid arch, as it does in Selachians. Thus in this respect, too, the conditions do not support the view put forward by Allis.



An account of the exact homologues of the basipterygoid process of the Coelacanthids is given by me in connection with the description of the myodome of *Saurichthys* (Stensiö, 1922 *b*), and on the same occasion I also had the opportunity of dealing with the myodome of the Coelacanthids. As it will perhaps be a long time before I can get enough money to print my work on the Saurichthyids, I have found it necessary to give here *in extenso* the considerations that I made there on the Coelacanthids.

"In the Coelacanthids (Stensiö, 1921, pp. 53-62, 91-96, 120-122; 1922 *a*, pp. 177-184, 205-206) there has taken place, in connection with the considerable growth of the eyes, a compression and thinning from the sides of certain postero-ventral parts of the orbito-temporal region and an adjacent smaller part of the

Text-figure 6.

*Diplocercides kayseri* (V. Koenen).

Median sagittal section through the neurocranium. Cartilaginous parts restored.  
Cartilage dotted, cartilage bone shaded. 2/1.

*Fr*, frontal part of the dermal cranial roof; *Ol*, occipito-labyrinth ossification; *Pa.it*, parieto-intertemporal; *Psp*, parasphenoid; *Sph*, sphenoid; *a.car.int*, unpaired canal for the internal carotid arteries; *bo*, basioccipital portion of the occipito-labyrinth ossification; *ch*, chorda space; *cv*, cranial cavity; *fen*, anterior division of the myodome; *f.hyp*, fossa hypophyseos; *my*, posterior division of the myodome; *s*, canal between the fossa hypophyseos and the myodome; *so*, supra-occipital portion of the occipito-labyrinth ossification.

labyrinth region. These thinned parts have a rather considerable fenestration close to the base of the primordial neurocranium, the orbits thus being in communication with each other at this place. The fenestration, the ventral boundary of which is formed by the parasphenoid, is situated ventrally of the fossa hypophyseos, with which it has presumably communicated, and just posterior to the unpaired canal for the arteriæ carotides internæ, that ascends vertically through the basis cranii, entering the cranial cavity immediately anterior to the fossa hypophyseos.

The fenestration has thus approximately the same position as the canalis transversus of the Elasmobranchii (canal for the pituitary vein), and must certainly be considered as such a canal, though it has become very much widened and in addition shortened in a transversal direction. From its posterior surface, which is somewhat wider than the anterior one, a short fossa penetrates in a backward direction between the base of the primordial neurocranium and the parasphenoid. To define it more closely, this fossa is so situated in the post-Devonian Cœlacanthids, that it is bounded dorso-caudally and caudally by the corpus of the basisphenoid and on either lateral side by the ventral process of the basisphenoid, while the ventral wall is formed by the parasphenoid. In the Devonian form *Diplocercides kayseri* (Stensiö, 1922 a, pp. 178-179, 205-206) the fossa is situated in quite the same place as in the post-Devonian forms, but as there the basisphenoid is contained in and forms a postero-ventral part of the large sphenoid, it is consequently bounded there dorsally, caudally, and laterally by the pars basisphenoidea sphenoides.

"In fishes in general, as we know, the recti muscles of the eye have their place of origin postero-ventrally of the opticus and oculomotorius foramina or else postero-ventrally of a line that can be drawn through these two foramina. In the Cœlacanthids the place where one must suppose the musculi recti to have originated is occupied by the widened transversal canal, and we can, therefore, scarcely help thinking that an expansion of this canal has been caused by the recti muscles. The recti externi have probably, as usual, invaded the transversal canal and then pushed postero-ventrally into the posterior wall of this canal, forming the short fossa described in this wall. The other three musculi recti have perhaps partly had their origin on some vertical membrane, which may have filled the anterior part of the transversal canal; most probably, however, they ought to have originated for the most part from the dorsal surface of the parasphenoid on the sides of or in the transversal canal itself. Whatever the conditions may have been with regard to the origin of certain of the recti muscles, it seems, however, impossible not to suppose that in the expanded transversal canal and the fossa opening into this from behind we are concerned with a sort of myodome."

"Watson has recently (1921, p. 335) doubted this explanation of mine, which I put forward in an incomplete form in the former part of this work. He then laid stress especially on the fact that the space that would be regarded as a myodome could not under any circumstances be homologous with the myodome of the Palæoniscids, which of course is situated dorsally of the basipterygoid process and laterally of what he calls 'the body of the basisphenoid.' It is of course true that the relation of the myodome to the basipterygoid process is quite different in Palæoniscids and Cœlacanthids, but, as I believe I can show,

this difference is due to the upward displacement of the articulation between the primordial neurocranium and the palato-quadrate in the Cœlacanthids (Stensiö, 1922*a*, pp. 205–206) from its original position at or near the base of the neurocranium.”

“For if we turn to *Dictyonosteus* we find there a large basiptyergoid process which certainly extends some distance upwards along the lateral surface of the neurocranium but which issues, however, also in part from the cranial base. This basiptyergoid process really forms, if one will so express it, a very powerful ‘wulst’ along the posterior edge of the sphenoid (*cf.* Stensiö, 1921, p. 56) where it begins immediately above the parasphenoid—*i. e.* at the basis cranii—and continues upwards and somewhat backwards to about a third of the height of the neurocranium at this place, ending there with a truncated upper end. On account of the oblique position of the process the anterior surface of this is directed antero-dorsally and the posterior one postero-ventrally. The process has in addition a dorsal surface and has certainly also had another one against which the metapterygoid probably articulated. This latter surface, which probably faced ventro-laterally and perhaps somewhat posteriorly, is, however, not well preserved.”

“The antero-dorsal surface of the basiptyergoid process and the lateral wall of the part of the sphenoid just in front of the basiptyergoid process in *Dictyonosteus* form together a sort of shallow antero-laterally and somewhat dorsally directed fossa at the inner end of which the well-developed canalis transversus opens. The vena jugularis has passed the opening of this canal and received the vena pituitaria from it, after which it has continued upwards and backwards in a very distinct sulcus on the boundary between the external vertical surface of the sphenoid and the antero-dorsal surface of the basiptyergoid process, until it reached the dorsal surface of the latter process, where it presumably turned more straight backwards, situated all the time close to the lateral surface of the sphenoid. The arteria carotis interna must in its forward course have been situated on the outside of the basiptyergoid process close to its base. At the anterior end of the basiptyergoid process it must have turned in a medial direction, entering a sphenoid by a large foramen. The parasphenoid lacks the processus ascendens, but if this had been developed the arteria carotis interna would have passed between it and the basiptyergoid process to its canal in the sphenoid just referred to.”

“From the upper end of the basiptyergoid process a ridge, which if not strong is still distinctly marked, passed upward and forward to the cranial roof; and just in front of this ridge, which I have called the alisphenoid ‘wulst,’ we find at the top not far below the cranial roof the anterior opening of a canal, which, as far as one can judge (*cf.* Stensiö, 1921, pp. 60, 93), must have

transmitted the n. ophthalmicus lateralis (*cf.* also Stensiö, 1921, p. 170) and lower, a short distance above the dorsal end of the basipterygoid process, the anterior opening of another canal, which seems to have transmitted their r. ophthalmicus profundus or some similar nerve."

"The main part of the trigeminus nerve, together with the lateralis nerves accompanying the trigeminus branches, has traversed the cranial wall rather high postero-dorsally of the basipterygoid process behind the alisphenoid wulst, and must then have run forward and a little downward dorsally of this process. The facialis exit must have been situated still somewhat farther backward, but at the same time certainly also more ventrally than the trigeminus exit. The r. palatinus facialis has been thence given off in a forward and downward direction, and it probably came down behind the basipterygoid process, afterwards turning in a forward direction on the outside of the basal part of this process. In this part of its course the r. palatinus facialis ought to have been situated, at least for some distance, rather close to the arteria carotis interna. The n. abducens probably accompanied the trigeminus branches, and thus passed dorsally of the basipterygoid process. Finally, it may also be pointed out that the large fossa hypophyseos reaches with its postero-ventral part into the part of the sphenoid situated between the basipterygoid processes."

"From the facts stated, it is obvious that the formation in *Dictyonosteus* that has hitherto been called the basipterygoid process must really in its antero-ventral part be homologous with a posterior larger part of the basipterygoid process in *Birgeria*, at the same time, however, also including something more than this. It would have about its entire correspondence in *Birgeria* if we supposed there the myodome half of one side with the exception of the prepituitary part to be filled out with bone and this bone-mass forming a connected whole with the basipterygoid process forward and downward, and also with the basal parts of sphenoid on the medial side. In a similar way it would have its equivalent in *Amia* if in this fish we supposed the lateral parts of the myodome of either side, apart from the prepituitary part, to be filled with bone or cartilage, but in this case of course it would correspond exactly only to the anterior part of such a bone or cartilage mass. In sharks it corresponds somewhat but not quite exactly to a posterior part of what Allis (1914 *a*) calls the 'subocular shelf'—together with an adjoining part of the capsula auditiva postero-ventrally of the vena jugularis. The correspondence would in the latter case be almost complete if only these cartilaginous parts in the sharks were developed somewhat more in such a way as to form a lateral wall, to some extent more complete, for the fossa at the posterior end of the orbit in which the canalis transversus opens out, and in which the trigeminus ganglionic complex is also usually



situated (fossa trigemino-pituitaria, Allis, 1914 *a*). The basipterygoid process is *Dictyonosteus* thus comprises not only the homologue to the actual basipterygoid process, but also certain other parts of the cranial wall."

"Dorsally of the upper end of the basipterygoid process—if we may, for the sake of brevity, retain the term basipterygoid process for it—*Dictyonosteus* lacks every equivalent to the outer wall of the trigemino-facialis chamber in *Birgeria*, *Amia*, *Lepidosteus*, and Teleosts, and also to the postorbital process and the sphenotic. As also no processus ascendens parasphenoidi that might have covered this part of the cranial wall is present, the trigemino-facialis chamber is consequently absolutely lacking. If a myodome were developed in *Dictyonosteus* this myodome would naturally be without lateral prespinal parts."

"In *Eusthenopteron* (Bryant, 1919, text-fig. 5; pl. ix. fig. 3) a basipterygoid process is found of essentially the same type as the one just described in *Dictyonosteus*. It only reached somewhat higher up than in the latter form. In a fossa between it and the vertical interorbital wall is situated the opening of the canalis transversus in the same way as in *Dictyonosteus*. By its greater extension upwards the basipterygoid process in *Eusthenopteron* shows a certain tendency to develop in the same direction as in the Cœlacanthids. For, if we imagine its ventral part reduced or weakly developed, the remaining dorsal part would evidently come to correspond fairly closely to the basipterygoid process in the Cœlacanthids, as I have already pointed out in another work (Stensiö, 1922 *a*, pp. 205–206). This means of course that the basipterygoid process of the Cœlacanthids would be homologous with at least a part of the septum that separates the myodome from either trigemino-facialis chamber in Teleosts."

"This view of the basipterygoid process in the Cœlacanthids is also supported by the course of the nerves and the vessels. In *Diplocercides kayseri*, where the conditions are best known, we thus find the following conditions (Stensiö, 1922 *a*). All the trigeminus branches except the r. ophthalmicus profundus must have passed forward dorsally of the basipterygoid process, as has the vena jugularis on its way backward after having received the v. pituitaria, which traversed the anterior part of the myodome from side to side. The r. palatinus facialis must in all probability on its way forwards and downwards have run just postero-ventrally of the so-called basipterygoid process, and probably reached down to the level of the cranial base just at the myodome. The arteria carotis interna must have had its course far ventrally of the so-called basipterygoid process, and has, as we have seen, entered the primordial neurocranium at the anterior end of the myodome, where it turned directly upwards in an unpaired canal which opened into the cranial cavity immediately behind the exits of the optic nerves. With regard to the n. abducens, it is true that as yet nothing certain



is known about it, but presumably it accompanied the trigeminus branches." \*

"The myodome in the Cœlacanthids as described here has pro-otic, pituitary, and prepituitary parts (*cf.* Allis, 1919). The pro-otic part of it is represented by the fossa situated between the basisphenoid (pars basisphenoidæa of the sphenoid in *Diplocercides*) and the parasphenoid. The pituitary part is situated beneath the fossa hypophyseos, and is separated from this fossa by a roof of bone pierced only by a small opening for the hypophysis. The prepituitary part is very short, and is only homologous with the median portion of the prepituitary part of the myodome in the Teleosts. Homologues to the lateral portions of the prepituitary part of the myodome in the Teleosts are totally lacking, even as potential."

"As at least in the fossil state of preservation the myodome in the Cœlacanthids is bounded directly by the parasphenoid on the ventral side, it might be supposed to consist of both a dorsal and a ventral compartment, like the myodome in the Teleosts. If this were actually the case, the ventral compartment must, however, at least in certain species (*Axelia*, Stensiö, 1921, p. 95), have been very short and limited only to the anterior end of the myodome, as the parasphenoid in these species (*Axelia*) beneath the middle and posterior parts of the myodome undoubtedly seems to comprise parts ossified in the ventral wall of the primordial neurocranium, and the parts so ossified there form the floor of the myodome." †

"The myodome in the Cœlacanthids can easily be thought to have arisen from the conditions in the Rhipidistids in the following way. If in the Rhipidistids the postero-ventral parts of the orbitotemporal region and the adjacent part of the labyrinth region became much compressed from the sides and thinned by an increase in the size of the eye-balls, the canalis transversus would of course be very much shortened. If, then, the muscoli recti externi invaded the opening of this shortened canal, they would rather soon meet with their origins in the median line, causing a considerable widening of the whole canal.

\* In my paper on the Devonian Cœlacanthids from Wildungen (Stensiö, 1922 a, p. 183), I was of the opinion that the n. abducens in *Diplocercides* ought to have run postero-ventrally of the so-called basiptyergoid process of the fish. The opinion maintained in the present work seems, however, more in agreement with the general conditions than my earlier one.

† "From the conditions described here in *Dictyonosteus* it is evident that the objections made by Allis, 1922 (pp. 149-152) against my interpretation of certain parts of the neurocranium in the Cœlacanthids must be untenable. There can be no doubt that the dorsal part of the basiptyergoid process of *Dictyonosteus* is homologous with the corresponding part of the process of *Eusthenoptern* and the whole process of the primitive Cœlacanthids (*Diplocercides*), and that accordingly also the jugular vein in this form has run dorsally of the process as it has done in *Dictyonosteus*. Among the post-Devonian Cœlacanthids we have in *Axelia* a form which with regard to the position of the basiptyergoid process shows rather intermediate conditions between the primitive Cœlacanthids (*Diplocercides*) and *Wimania*, in which latter the process issues very high above the cranial base."

Being forced to shift their origins still farther backwards by the continued growth of the eye-bulbs, the recti externi muscles may be imagined to have pushed backwards into the posterior wall of the transversal canal, forming a fossa there opening in front into the transverse canal. Then, perhaps chiefly owing to the influence of the other recti muscles, a widening of the transverse canal forward may be supposed to have taken place at the expense of the bone part between this canal and the vertically ascending canal for the internal carotid arteries. Finally, the transverse canal, by the influence of the recti muscles, grew wider downwards as well, the floor of the canal belonging to the primordial neurocranium at the same time becoming much reduced, and finally perhaps forming only a membrane on the dorsal surface of the parasphenoid. The recti inferiores, posteriores, and superiores can after this have been able more or less easily to break through the membrane with their origins in seeking a firm attachment on the parasphenoid, and if this had happened a ventral myodomic compartment would have arisen. That a myodome arisen in the way sketched here from the conditions in the Rhipidistids must lack homologues of the lateral portions of the prepituitary parts of the myodome in *Birgeria*, *Amia*, and Teleosts, as the myodome in the Coelacanthids actually does, is evident from what has been put forward above concerning the Rhipidistids."

"In this connection finally it ought also to be pointed out that the occurrence of a myodome in the Coelacanthids shows with full certainty that a myodome can easily develop, and that the myodome in several groups of fishes has been developed independently."

"The myodome in the Coelacanthids, if it has no ventral compartment, would, as is easily understood, correspond fairly well to the myodome in *S. ornatus* if the latter were extended forward by reduction of the larger posterior part of the bone-part *bsph*."

If we summarize here the results obtained by the investigation of the Coelacanthids with regard to the basipterygoid process, we find the following. The basipterygoid process of the primitive ancestors of the Coelacanthids must have been rather high, extending upwards along the lateral side of the primordial neurocranium as in *Dictyonosteus*, and the metapterygoid probably articulated against the upper parts of this process. Through reduction of the ventral parts of the process the conditions which occur in *Diplocercides* seem to have arisen, and from these the evolution towards the post-Devonian Coelacanthids ought to have proceeded in such a way that the parts of the cranial basis below the remains of the basipterygoid process grew very deep, while at the same time the height of the parts dorsally of this process decreased.

In *Diplocercides* the sphenoid, like that of the Rhipidistids, comprises paired orbitosphenoid and alisphenoid components and an unpaired basisphenoid component. In the post-Devonian

forms, on the other hand, there are found merely posterior parts of the basisphenoid and alisphenoid components, while the anterior parts of these components, together with the orbito-sphenoid component, have been reduced and replaced by cartilage.

In *Macropoma* the part present of the alisphenoid component of either side is continuous with the basisphenoid component, thus having there its original relation to the latter component (Watson, 1921, p. 323). In *Azelia* and *Wimania*, on the other hand, the alisphenoid component of each side has coalesced with and forms a descending process from the fronto-dermosphenotic of its side. These different conditions of the alisphenoid component in different forms are of very great interest, as they show that a part of a substitution bone may rather easily become independent and coalesce with other neighbouring bones, even dermal ones (*cf.* Stensiö, 1921, pp. 153-161, 181-182; Allis, 1899, 1909).

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## EXPLANATION OF THE PLATE.

- Fig. 1. *Dictyonosteus arcticus* Stensiö. Anterior half of the neurocranium in lateral view. The lateral parts of the ethmoidal region and of the cranial roof removed. 1/2.
- Fig. 2. *Dictyonosteus arcticus* Stensiö. Same parts as in the preceding figure, but with the basipterygoid process removed to show the canal for the pituitary vein and the fossa hypophyseos. 1/2.
- Fig. 3. *Dictyonosteus arcticus* Stensiö. Sphenoid from behind. 1/2.
- Fig. 4. *Dictyonosteus arcticus* Stensiö. Antero-lateral view of the posterior half of the sphenoid. N.B. The very distinct sulcus for the jugular vein (*sj*), and the opening of the canal for the pituitary vein (*v.pit*). 1/2.
- Fig. 5. *Porolepis* ? sp. Anterior part of the dermal cranial roof, showing the sensory canals.

The type-specimen of figs. 1-4 belongs to the Palæontological Institution, Upsala the type-specimen of fig. 5 to the Palæontological Museum, Christiania.

*Index letters.*

*E.pethm*, exethmoideo-preëthmoid; *Fr*, frontal; *Psph*, parasphenoid; *Sph*, sphenoid; *a.car.int*, canal for the arteria carotis interna; *alsph*, alisphenoid wulst; *bp*, basipterygoid process; *cn*, orbito-nasal canal for vessels to or from, or both to and from the nasal pit; *c.ophtl.lat*, through the dorsal part of the alisphenoid wulst for the n. ophthalmicus lateralis; *cv*, cranial cavity; *f.hyp*, fossa hypophyseos; *ifc*, infraorbital sensory canal; *sj*, sulcus for the vena jugularis; *soc*, supraorbital sensory canal; *v.cerebr.ant*, canal for the anterior cerebral vein; *v.pit*, canal for the pituitary vein; I, olfactory canal; II, opticus canal; III, oculomotorius canal; IV, trochlearis canal; V, trigeminus exit; *V<sub>1</sub>*, canal for the r. ophthalmicus profundus.





## EXHIBITIONS AND NOTICES.

October 24th, 1922.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the months of June, July, August, and September, 1922 :—

## JUNE.

The registered additions to the Society's Menagerie during the month of June were 157 in number. Of these 75 were acquired by presentation, 34 were deposited, 26 were purchased, and 22 were born in the Menagerie.

The following may be specially mentioned :—

1 Striped Hyæna (*Hyæna hyæna*), from Kaduna, Nigeria, presented by Lt. L. S. Clinton on June 20th.

3 Cape Hyraxes, born in the Menagerie on June 19th.

1 Greater Amethyst Sun-bird (*Chalcomitra amethystina*) and 1 Malachite Sun-bird (*Nectarinia famosa*), from South Africa, presented by Mrs. George Robey on June 6th.

1 Apure Tovi Parrakeet (*Brotogerys jugularis apurensis*), from Apure, Venezuela, new to the Collection, presented by Mons. J. Delacour, F.Z.S., on June 12th.

6 Pink-winged Rose-Finches (*Rhodospiza obsoleta*), from Persia, presented by Alfred Ezra, O.B.E., F.Z.S., on June 12th.

1 White-crested Hornbill (*Ortholophus leucolophus*), from Coomassie, West Africa, new to the Collection, presented by Major Harold W. Sidley on June 12th.

A collection of Indian Snakes, including 2 Hamadryads (*Naia bungarus*), presented by Alfred Ezra, O.B.E., F.Z.S., on June 12th.

A Tiger-Fish (*Carapus fasciatus*), from Brazil, new to the Collection, purchased on June 15th.

## JULY.

The registered additions to the Society's Menagerie during the month of July were 229 in number. Of these 120 were acquired by presentation, 17 were deposited, 31 were purchased, 1 was received in exchange, and 60 were born in the Menagerie.

The following may be specially mentioned :—

1 Tiger (*Felis tigris*), ♂, from Bhopal, Central India, presented by H.H. Raja Sir Birandra Singh, K.C.I.E., on July 13th.

1 Kiang (*Equus kiang*), ♀, born in the Menagerie on July 9th.

2 Guinea Baboons (*Papio papio*), 1 African Civet (*Civettictis civetta*), 2 African Porcupines (*Hystrix africa-australis*), 2 Harnessed Antelopes (*Tragelaphus scriptus*), 1 Saddle-billed Stork (*Ephippiorhynchus senegalensis*) from Gambia, and 3 Ostriches

(*Struthio camelus*) from Senegal: presented by H.E. Capt. C. H. Armitage, C.M.G., D.S.O., on July 18th.

1 Chestnut-capped Buarremon (*Buarremon brunneinucha*), from Southern Mexico, new to the Collection, purchased on July 25th.

1 White-bellied Amethyst Starling (*Pholidauges leucogaster*),

2 Broad-tailed Babblers (*Crateropus platycercus*), presented by Dr. E. Hopkinson, C.M.G., D.S.O., on July 17th.

A Grooved Tortoise (*Testudo calcarata*), bred in the Menagerie on July 16th.

A West-African Chameleon (*Chamæleon gracilis*), new to the Collection, presented by H.E. Capt. C. H. Armitage, C.M.G., D.S.O., on July 18th.

#### AUGUST.

The registered additions to the Society's Menagerie during the month of August were 187 in number. Of these 102 were acquired by presentation, 42 were deposited, 25 were purchased, 3 were received in exchange, and 15 were born in the Menagerie.

The following may be specially mentioned:—

1 Brazilian Tapir (*Tapirus terrestris*), from Brazil, deposited on August 29th.

16 Prairie-Marmots (*Cynomys ludovicianus*), from North America, purchased on August 22nd.

2 Pocket-Gophers (*Thomomys bulbivorus*), from San Francisco, new to the Collection, deposited on August 15th.

3 Greater Amethyst Sun-birds (*Chalcomitra amethystina*), from Durban, presented by A. M. Campbell, F.Z.S., on August 13th.

1 Verreaux's Amethyst Starling (*Pholidauges leucogaster verreauxi*), from Durban, presented by Harold Millar, C.M.Z.S., on August 13th.

A young Wart-Hog (*Phacochoerus africanus*) and a collection of Reptiles, including 2 Green Tree-Snakes (*Chlorophis irregularis*) and a Skink (*Chalcides*, sp. nova), both new to the Collection, from Gambia, presented by H.E. Capt. C. H. Armitage, C.M.G., D.S.O., F.Z.S., on August 15th.

1 Mamba (*Dendraspis angusticeps*), new to the Collection, from South Africa, purchased on August 11th.

13 Buerger's Tree-Frogs (*Rhacophorus buergeri*), new to the Collection, from Japan, presented by Mr. Tomisaburo Nagai.

2 Sucker-Fish (*Plecostomus commersoni*), new to the Collection, from South America, purchased on August 31st.

#### SEPTEMBER.

The registered additions to the Society's Menagerie during the month of September were 214 in number. Of these 87 were acquired by presentation, 17 were deposited, 62 were purchased, 19 were received in exchange, and 29 were born in the Menagerie.

The following may be specially mentioned:—

2 Musk-Oxen (*Ovibos moschatus*), ♂ ♀, from Greenland, purchased on September 19th.

1 Tigress (*Felis tigris*), from Perak, presented by W. H. Jones, Esq., on September 18th.

2 Cheetahs (*Cynelurus jubatus*), from Nairobi, deposited on September 25th.

1 Nagor Antelope (*Redunca nagor*), 1 Gambian Oribi (*Ourebia nigricaudata*), 3 Petas Cercopithecues (*Cercopithecus patas*), 3 Nilotic Monitors (*Varanus niloticus*), 1 West-African Chameleon (*Chamaleon gracilis*), 1 Hissing Sand-Snake (*Psammodphis sibilans*), and 1 Senegal River-Turtle (*Cyclanorbis senegalensis*), from Gambia, presented by H.E. Capt. C. H. Armitage, C.M.G., D.S.O., F.Z.S., on September 19th.

1 Spectacled Owl (*Pulsatrix perspicillata*), from South America, purchased on September 18th.

1 Rock-Bunting (*Fringillaria tahapizi*), from South Africa, new to the Collection, presented by the Hon. Mrs. Charles Winn on September 26th.

A large collection of N.-American Snakes, including 2 Copper Heads (*Ancistrodon contortrix*), a Confluent Rattlesnake (*Crotalus confluentus*), and a Horned Rattlesnake (*Crotalus horridus*), presented by Dr. Howard A. Kelly on September 11th.

2 Puff-Adders and a Reinhardt's Snake (*Prosymna meleagris*), the latter new to the Collection, from Mongalla, Sudan, presented by the Rev. A. Shaw, C.M.G., on September 2nd.

The SECRETARY exhibited, and made remarks upon, two photographs of Zebras and Oryx from Kenya.

MR. E. T. NEWTON, F.R.S., F.Z.S., exhibited, and made remarks upon, the tanned skin of a Frog.

MR. C. TATE REGAN, F.R.S., F.Z.S., exhibited, and made remarks upon, some specimens of leather made from Sharks' skins.

### November 7th, 1922.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,  
in the Chair.

Prof. G. ELLIOT SMITH, M.D., F.R.S., F.Z.S., exhibited, and made remarks upon, a series of photographs of a fossil tooth (*Hesperopithecus*) from Nebraska.

Dr. A. SMITH WOODWARD, F.R.S., F.Z.S., exhibited, and made remarks upon, drawings and photographs comparing teeth of a Bear, Chimpanzee, and *Hesperopithecus*.

November 21st, 1922.

Sir S. F. HARMER, K.B.E., F.R.S., Vice-President,  
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of October, 1922 :—

The registered additions to the Society's Menagerie during the month of October were 263 in number. Of these 172 were acquired by presentation, 40 were deposited, 21 were purchased, 8 were received in exchange, and 22 were born in the Menagerie.

The following may be specially mentioned :—

2 American Bisons (*Bison americanus*), ♂ ♀, from Canada, presented by the Canadian Government on October 23rd.

1 Pygmy African Elephant (*Loxodon cyclotis*), ♀, from French Gaboon, deposited on October 16th.

1 Black-throated Saltator (*Saltator aratricollis*), from Bahia, Brazil, new to the Collection, purchased on October 26th.

7 Cream-coloured Coursers (*Cursorius gallicus*), from Egypt, new to the Collection, purchased on October 4th.

2 Black Storks (*Ciconia nigra*), from Poland, presented by H.S.H. Prince Charles Radziwill on October 25th.

1 Kea Parrot (*Nestor notabilis*), from New Zealand, presented by Lady Ursula Abbey on October 4th.

49 Indian Fruit-Bats (*Pteropus medius*) and a collection of Indian Reptiles, including 2 Cobras, a Russell's Viper, and a Banded Krait, presented by A. Ezra on October 7th.

A collection of rare tropical fish including several species new to the Collection, presented by J. R. Shattock on October 8th.

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Prof. E. W. MACBRIDE, F.R.S., F.Z.S., exhibited, and made remarks upon, a series of lantern-slides bearing upon Dr. Kammerer's experiments on Amphibia.

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Dr. A. SMITH WOODWARD, F.R.S., F.Z.S., exhibited, and made remarks upon, a skull and tusks of a Mammoth from Siberia, and drew attention to the remarkably perfect and fresh condition of the specimen.

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Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, the shed lining of the gizzard of a Hornbill.



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

February 7th, 1922.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

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The SECRETARY read a Report upon the Additions to the Society's Menagerie during the months of November and December, 1921.

Mr. A. H. EVANS, F.Z.S., exhibited, and made remarks upon, a series of Cuckoos' eggs taken near Cambridge.

Mr. C. W. HOBLEY, C.M.G., C.M.Z.S., gave a *résumé* of his paper on "The Fauna of East Africa and its Future," and drew special attention to the urgent need for immediate action being taken, if the rapidly disappearing herds of Big Game are to be preserved from total extinction.

Lord CLIFFORD OF CHUDLEIGH, F.Z.S., exhibited, and made remarks upon, a series of photographs of *Nototherium mitchelli*.

Miss L. E. CHEESMAN, F.E.S., gave an account of the position and function of the Siphon in the Amphibious Mollusc *Ampullaria vermiciformis*.

Mr. G. C. ROBSON, F.Z.S., exhibited, and made remarks upon, a series of models demonstrating the respiratory mechanism of *Ampullaria vermiciformis*.

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In the absence of Lt.-Col. J. STEPHENSON, D.Sc., F.Z.S., his communication "Contribution to the Morphology, Classification, and Zoogeography of Indian Oligochaeta:—

IV. On the diffuse Production of Sexual Cells in a Species of *Chaetogaster* (Fam. Naididae).

V. On *Drawida japonica* (Michlson.), a Contribution to the Anatomy of the Moniligastridae.

VI. On the Relationships of the Genera of Moniligastridae; with some Considerations on the Origin of Terrestrial Oligochaeta,"  
was taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, February 21st, at 5.30 P.M., when the following communications will be made:—

R. BROOM, D.Sc., F.R.S., C.M.Z.S.

On the Temporal Arches of the Reptilia.

H. BLEGVAD, Ph.D.

Animal Communities in the Southern North Sea.

CHAS. F. SONNTAG, M.D., F.Z.S.

(1) On the Vagus and Sympathetic Nerves of the Edentata.

(2) On the Vagus and Sympathetic Nerves of *Hyraax capensis*.

C. TATE REGAN, F.R.S., F.Z.S.

The Cichlid Fishes of Lake Victoria.

The following Papers have been received:—

F. BALFOUR BROWNE, M.A., F.Z.S.

The Life-history of the Water-Beetle *Pelobius tardus* Herbst.

EKENDRANATH GHOSH, M.D., M.Sc., F.R.M.S.

On the Animal of *Scaphula* Benson, with the Description of a new Species.

F. W. URICH, HUGH SCOTT, M.A., D.Sc., and J. WATERSTON,  
D.Sc., F.Z.S.

Note on the Bat-Parasite *Cyclopodia greeffi*, and on a new Species of Hymenopterous (Chalcid) Parasite bred from it.

S. K. MONTGOMERY, B.A., B.Sc.

Direct Development in a Dromiid Crab.

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**The Publication Committee desire to remind Fellows that it is only by courtesy that they are allowed to bring guests to a Scientific Meeting. For the present no Fellow can be permitted to bring more than one guest to a Meeting.**

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,  
*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,  
REGENT'S PARK, LONDON, N.W. 8.  
*February 14th, 1922.*



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

February 21st, 1922.

Prof. E. W. MACBRIDE, D.Sc., LL.D., F.R.S., Vice-President,  
in the Chair.

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The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of January, 1922.

The SECRETARY exhibited, and made remarks upon, a photograph of the Society's Gardens taken from an aeroplane.

Miss L. E. CHEESMAN, F.E.S., exhibited specimens of the Amphibious Mollusc, *Ampullaria vermiciformis*, and described the position and function of the siphon.

Mr. G. C. ROBSON, F.Z.S., exhibited a series of models demonstrating the respiratory mechanism of *Ampullaria vermiciformis*.

Mr. F. MARTIN DUNCAN, F.R.M.S., F.Z.S., exhibited a series of cinematograph films showing the movements of *Ampullaria vermiciformis*; of the Fresh-water Crab, *Cardisoma armatum*; and of the Hawk's-bill Turtle, *Chelonia imbricata*.

Miss L. E. CHEESMAN, F.E.S., described the habits, in captivity, of the Fresh-water Crab, *Cardisoma armatum*.

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Dr. E. S. RUSSELL, F.Z.S., communicated a paper by Dr. H. BLEGVAD on "Animal Communities in the Southern North Sea."

Mr. C. TATE REGAN, F.R.S., F.Z.S., gave a *résumé* of his paper on "The Cichlid Fishes of Lake Victoria."

Dr. CHAS. F. SONNTAG, F.Z.S., gave a *résumé* of his papers "On the Vagus and Sympathetic Nerves of the Edentata" and "On the Vagus and Sympathetic Nerves of *Hyrax capensis*."

The next Meeting of the Society for Scientific Business will be held on Tuesday, March 7th, 1922, at 5.30 P.M., when the following communications will be made:—

N. S. LUCAS, M.B., F.Z.S., Pathologist to the Society.

Report on the Deaths which occurred in the Society's Gardens during 1921.

F. BALFOUR BROWNE, M.A., F.Z.S.

The Life-history of the Water-Beetle *Pelobius tardus* Herbst.

R. BROOM, D.Sc., F.R.S., C.M.Z.S.

On the Temporal Arches of the Reptilia.

F. W. URICH, HUGH SCOTT, M.A., D.Sc., and J. WATERSTON,  
D.Sc., F.Z.S.

Note on the Bat-Parasite *Cyclopodia greeffi*, and on a new Species of Hymenopterous (Chalcid) Parasite bred from it.

S. K. MONTGOMERY, B.A., B.Sc.

Direct Development in a Dromiid Crab.

The following Papers have been received:—

GILBERT BLAINE, F.Z.S.

Notes on the Zebras and some Antelopes of Angola.

R. I. Pocock, F.R.S., F.Z.S.

On the External Characters of some Hystricomorph Rodents.

H. R. Hogg, M.A., F.Z.S.

Some Spiders from South Annam.

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*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

*February 28th, 1922.*



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

March 7th, 1922.

Sir SIDNEY F. HARMER, K.B.E., F.R.S., Vice-President,  
in the Chair.

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Mr. C. TATE REGAN, F.R.S., F.Z.S., exhibited, and made remarks upon, some living specimens of the Indian Tortoise-Beetle *Aspidomorpha sanctæ-crucis*.

Mr. N. S. LUCAS, M.B., F.Z.S., read a Report on the Deaths which had occurred in the Society's Gardens during 1921.

Prof. D. M. S. WATSON, F.Z.S., gave a *résumé* of Dr. R. BROOM's paper "On the Temporal Arches of the Reptilia."

Dr. J. WATERSTON, F.Z.S., gave a *résumé* of a paper by F. V. URICH, H. SCOTT, and J. WATERSTON on "The Bat-Parasite *Cyclopodia greeffi*, and on a new Species of Hymenopterous (Chalcid) Parasite bred from it."

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Mr. S. V. MONTGOMERY, B.A., B.Sc., communicated his paper  
 "Direct Development in a Dromiid Crab."

In the absence of the Author, Mr. F. BALFOUR-BROWN's paper  
 on "The Life-History of the Water-Beetle, *Pelobius tardus*  
 Herbst," was taken as read.

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The next Meeting of the Society for Scientific Business will  
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R. I. Pocock, F.R.S., F.Z.S.

On the External Characters of some Histricomorph Rodents.

H. R. Hogg, M.A., F.Z.S.

Some Spiders from South Annam.

---

The following Papers have been received:—

J. T. CUNNINGHAM, M.A., F.Z.S.

Mendelian Experiments on Fowls.—III. Production of  
 Dominant Pile Colour.

M. KHALIL, M.D., D.P.H.

A Review of the Nematode Parasites of Elephants, with a  
 Description of Four new Species.

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ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

March 21st, 1922.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

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The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of February, 1922.

The SECRETARY read a short paper entitled "Monkeys and the Fear of Snakes," and, in illustration, exhibited a cinematograph film recently taken in the Society's Gardens by Mr. F. Martin Duncan, showing a young Chimpanzee playing with a live snake.

Mr. GILBERT BLAINE, F.Z.S., communicated his paper "Notes on the Zebras and some Antelopes of Angola."

Mr. R. I. POCKOCK, F.R.S., F.Z.S., gave a *résumé* of his paper "On the External Characters of some Histricomorph Rodents."

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Mr. H. R. HOGG, M.A., F.Z.S., gave a *résumé* of his paper  
 "Some Spiders from South Annam."

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The next Meeting of the Society for Scientific Business will be held on Tuesday, April 4th, at 5.30 P.M., when the following communications will be made :—

Mr. C. TATE REGAN, F.R.S., F.Z.S.

Exhibition of lantern-slides illustrating blind fresh-water Fishes from caves.

J. T. CUNNINGHAM, M.A., F.Z.S.

Mendelian Experiments on Fowls.—III. Production of Dominant Pile Colour.

M. KHALIL, M.D., D.P.H.

A Revision of the Nematode Parasites of Elephants, with a Description of Four new Species.

---

The following Papers have been received :—

R. J. ORTLEPP, M.A.

A new Species of the Nematode *Esophagostomum* from the Rodent *Xerus setosus*.

Miss L. E. CHEESMAN, F.E.S.

Observations on the Fresh-water Crab *Cardisoma armatum*, with especial regard to the Sense-organs.

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The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

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P. CHALMERS MITCHELL,

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ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

*March 28th, 1922.*





ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

April 4th, 1922.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,  
in the Chair.

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Mr. C. TATE REGAN, F.R.S., F.Z.S., exhibited, and made remarks upon, a series of lantern-slides illustrating specimens of various blind fresh-water Fishes from caves.

Mr. R. H. BURNE, M.A., F.Z.S., exhibited, and made remarks upon, specimens demonstrating the recessus orbitalis in Flat Fishes.

Mr. L. T. HOGBEN, B.A., F.Z.S., exhibited living specimens, and made remarks upon the influence of pituitary gland in inducing metamorphosis of the Axolotl.

Mr. J. T. CUNNINGHAM, M.A., F.Z.S., communicated his paper on "Mendelian Experiments on Fowls.—III. Production of Dominant Pile Colour."

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Dr. M. KHALIL, D.P.H., gave a *résumé* of his paper "A Revision of the Nematode Parasites of Elephants, with a Description of Four new Species.

The next Meeting of the Society for Scientific Business will be held on Tuesday, April 25th, at 5.30 P.M., when the following communications will be made:—

The SECRETARY.

Report on the Additions to the Society's Menagerie during the month of March, 1922.

R. J. ORTLEPP, M.A.

A new Species of the Nematode *Æsophagostomum* from the Rodent *Xerus setosus*.

CHAS. F. SONNTAG, M.D., F.Z.S.

On the Anatomy of the Drill (*Mandrillus leucophaeus*).

Dr. R. BROOM, F.R.S., C.M.Z.S.

On the Persistence of the Mesopterygoid in certain Reptilian Skulls.

ARTHUR LOVERIDGE.

New Reptiles from Tanganyika Territory.

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The following Papers have been received:—

ERNEST A. ELLIOTT, F.E.S., F.Z.S.

Monograph of the Family of the Stephanidæ (Diptera).

D. W. DEVANESEN, M.A.

Notes on the Anatomy of *Cacopus systoma*, an Indian Toad of the Family Engystomatidæ.

Miss L. E. CHEESMAN, F.E.S.

Observations on the Fresh-water Crab *Cardisoma armatum*, with especial regard to the Sense-organs.

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The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited as far as possible to the description of new results.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,  
*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,  
REGENT'S PARK, LONDON, N.W. 8.  
*April 11th, 1922.*





ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

April 25th, 1922.

Sir S. F. HARMER, K.B.E., F.R.S., Vice-President,  
in the Chair.

The SECRETARY read a Report upon the Additions to the Society's Menagerie during the month of March 1922.

The SECRETARY exhibited, and made remarks upon, some dressed skins of a Tree-Hyrax (*Procavia valida*?) from Tanganyika Territory.

Prof. P. T. FLYNN exhibited, and made remarks upon, a cast of the skull of a Squalodont Whale from the Tertiary (Miocene) Strata, Table Cape, Tasmania.

The SECRETARY communicated, on behalf of Mr. ARTHUR LOVERIDGE, C.M.Z.S., an account of Mr. Loveridge's experiences while watching "Lions at their Kill."

Mr. R. J. ORTLEPP, M.A., communicated his paper on "A new Species of the Nematode Genus *Esophagostomum* from the Rodent *Xerus setosus*."

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\* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Prof. D. M. S. WATSON, F.Z.S., gave a *résumé* of Dr. R. BROOM's paper "On the Persistence of the Mesopterygoid in certain Reptilian Skulls."

Dr. CHAS. F. SONNTAG, F.Z.S., communicated his paper "On the Anatomy of the Drill (*Mandrillus leucopneus*)."

Mr. ARTHUR LOVERIDGE's paper on "New Reptiles from Tanganyika Territory," and Miss L. E. CHEESMAN's paper "Observations on the Land-Crab, *Cardisoma armatum*, with especial regard to the Sense Organs," were taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, May 9th, at 5.30 P.M., when the following communications will be made:—

CHAS. F. SONNTAG, M.D., F.Z.S.

Exhibition of lantern-slides and specimens illustrating some points in the Anatomy and Physiology of Whales.

CHAS. F. SONNTAG, M.D., F.Z.S.

The Comparative Anatomy of the Tongues of the Mammalia.—VII. Cetacea, Sirenia, and Ungulata.

D. W. DEVANESEN, M.A.

Notes on the Anatomy of *Cacopus systoma*, an Indian Toad of the Family Engystomatidæ.

ERNEST A. ELLIOTT, F.Z.S., F.E.S.

Monograph of the Family of the Stephanidæ (Hymenoptera).

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The following Paper has been received :—

J. H. LLOYD, M.Sc., F.Z.S., and EDITH M. SHEPPARD, B.Sc., F.Z.S.

A Contribution to the Anatomy of a Hammerhead Shark  
(*Zygæna malleus*).

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The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,  
REGENT'S PARK, LONDON, N.W. 8.  
May 2nd, 1922.



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

May 9th, 1922.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

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The SECRETARY exhibited, and made remarks upon, a medal struck to commemorate the 150th Anniversary of the Royal Academy of Belgium.

Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, a series of cinematograph-films illustrating various stages in the life-history of the Wood-Ant (*Formica rufa*) and of the Common Wasp (*Vespa germanica*), and asked the Society to accept the series for its Zoological Film Library.

Dr. CHAS. F. SONNTAG, F.Z.S., exhibited, and made remarks upon, a series of specimens and lantern-slides illustrating some points in the Anatomy and Physiology of Whales.

Dr. CHAS. F. SONNTAG, F.Z.S., gave a *résumé* of his paper "The Comparative Anatomy of the Tongues of the Mammalia.—VII. Cetacea, Sirenia, and Ungulata."

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\* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.



Mr. D. W. DEVANESEN, M.A., communicated his paper "Notes on the Anatomy of *Cacopus systoma*, an Indian Toad of the Family Engystomatidæ.

In the absence of the Author, Mr. E. A. ELLIOTT's paper, "Monograph of the Family of the Stephanidæ (Hymenoptera)," was taken as read.

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The next Meeting of the Society for Scientific Business will be held on Tuesday, May 23rd, 1922, at 5.30 P.M., when the following communications will be made:—

The SECRETARY.

Report on the Additions to the Society's Menagerie during the month of April, 1922.

Rev. H. N. HUTCHINSON, M.A., F.Z.S., and ED. GODWIN.

Exhibition of a plaster cast of a model reconstruction of the marine reptile *Peloneustes philarchus*, a Pliosaur from the Oxford Clay.

Sir SIDNEY F. HARMER, K.B.E., F.R.S., Vice-President.

On Commerson's Dolphin and other Species of *Cephalorhynchus*.

C. FORSTER COOPER, M.A., F.Z.S.

Miocene Proboscidea from Baluchistan.

R. I. POCKOCK, F.R.S., F.Z.S.

On the External Characters of *Scarturus* and other Jerboas compared with those of *Zapus* and *Pedetes*.

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The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

*May 16th, 1922.*



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

May 23rd, 1922.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

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The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of April, 1922.

Mr. R. I. POCKOCK, F.R.S., F.Z.S., exhibited, and made remarks upon, a living example of the rare Bush-Dog *Speothos venaticus*.

Mr. E. G. BOULENGER, F.Z.S., and Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, a Cinematograph record which they had taken illustrating the Life-history of the Axolotl (*Amblystoma tigrinum*).

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, a series of photographs he had taken of some recent important additions to the Society's collection of Birds.

The Rev. H. N. HUTCHINSON, M.A., F.Z.S., exhibited, and made remarks upon, a plaster cast of a model reconstruction of the marine reptile *Peloneustes philarchus*, a Pliosaur from the Oxford Clay, stating that he had received valuable assistance from Mr. Ed. Godwin in completing the model.

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\* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Sir SIDNEY F. HARMER, K.B.E., F.R.S., communicated his paper "On Commerson's Dolphin and other Species of *Cephalorhynchus*."

Mr. C. FORSTER COOPER, M.A., F.Z.S., gave a résumé of his paper on "Miocene Proboscidea from Baluchistan."

Mr. R. I. POCKOCK's papers, "On the External Characters of *Scarturus* and other Jerboas compared with those of *Zapus* and *Pedetes*," was taken as read.

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The next Meeting of the Society for Scientific Business will be held on Tuesday, June 13th, 1922, at 5.30 P.M., when the following communications will be made:—

THE SECRETARY.

On the Council's scheme to establish an Aquarium in the Society's Gardens.

MISS JOAN B. PROCTOR, F.Z.S.

A Study of the Tortoise *Testudo loveridgii*, Blgr., and the Morphogeny of the Chelonian Carapace.

J. T. CARTER, F.Z.S.

A Microscopical Examination of the teeth of the Primates.

HAROLD G. JACKSON, M.Sc., F.Z.S.

A Revision of the Isopod Genus *Ligia* (*Fabricus*).

W. R. B. OLIVER, F.L.S., F.Z.S.

A Review of the Cetacea of the New Zealand Seas.

Prof. WOOD JONES, F.Z.S.

On the Dental Characters of certain Australian Rats.

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The following papers have been received :—

ANAND KUMAR, M.A.

A new Variety of *Rhabdocynthis pallida*.

J. H. LLOYD, M.Sc., F.Z.S., and EDITH M. SHEPPARD, B.Sc.,  
F.Z.S.

A Contribution to the Anatomy of a Hammerhead Shark  
(*Zygæna mollus*).

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The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

May 30th, 1922.



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

June 13th, 1922.

Prof. E. W. MACBRIDE, D.Sc., LL.D., F.R.S., Vice-President,  
in the Chair.

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The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of May, 1922.

Miss JOAN B. PROCTER, F.Z.S., communicated her paper, "A Study of the remarkable Tortoise *Testudo loveridgii* Blgr., and the Morphogeny of the Chelonian Carapace."

Mr. J. T. CARTER, F.Z.S., gave a *résumé* of his paper, "A Microscopical Examination of the Teeth of the Primates."

Mr. HAROLD G. JACKSON, M.Sc., F.Z.S., gave a *résumé* of his paper on "A Revision of the Isopod Genus *Ligia* Fabricius."

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In the absence of the Authors, Mr. W. R. B. OLIVER's paper, "A Review of the Cetacea of the New Zealand Seas," and Prof. F. WOOD JONES's paper, "On the Dental Characters of certain Australian Rats," were taken as read.

The SECRETARY briefly described the technical side of the Council's scheme to establish an Aquarium in the Society's Gardens.

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The next Meeting of the Society for Scientific Business will be held on Tuesday, October 24th, at 5.30 P.M.

A notice stating the Agenda for the Meeting will be circulated early in October.

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The following Papers have been received:—

R. C. BANKS.

On a possible Geological Cause of Colour Variation in Animals.

E. LEONARD GILL, M.A.

The Permian Fishes of the Genus *Acentrophorus*.

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The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

*June 20th, 1922.*





ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

October 24th, 1922.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

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The SECRETARY read a Report on the Additions to the Society's Menagerie during the months of June, July, August, and September, 1922.

The SECRETARY exhibited, and made remarks upon, two photographs of Zebras and Oryx from Kenya.

Mr. E. T. NEWTON, F.R.S., F.Z.S., exhibited, and made remarks upon, the tanned skin of a Frog.

Mr. C. TATE REGAN, F.R.S., F.Z.S., exhibited, and made remarks upon, some specimens of leather made from Sharks' skins.

A paper on "The Fœtal Membranes and Placentation of *Chiromys madagascariensis*," by Prof. J. P. HILL, F.R.S., F.Z.S., and Mr. R. H. BURNE, M.A., F.Z.S., was communicated by Prof. J. P. HILL.

Mr. R. I. Pocock, F.R.S., F.Z.S., described the external characters of the fœtus of *Chiromys madagascariensis*.

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A paper by Mr. R. KIRKPATRICK, F.Z.S., and Dr. J. METZELAAR, "On an Instance of Commensalism between a Hermit-Crab and a Polyzoön," was communicated by Mr. KIRKPATRICK.

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The next Meeting of the Society for Scientific Business will be held on Tuesday, November 7th, 1922, at 5.30 P.M., when the following communications will be made:—

C. S. ELTON.

On the Colours of Water-Mites.

E. B. POULTON, M.A., F.R.S., F.Z.S.

Experimental evidence that commensalism may be beneficial to Crustacea.

G. M. VEVERS, M.R.C.S., L.R.C.P., F.Z.S.

Nematode Parasites of Mammals from the Zoological Society.

W. J. KAYE, F.E.S.

New Species of Trinidad Moths.

CHAS. F. SONNTAG, M.D., F.Z.S.

On the Myology and Classification of the Wombat, Koala, and Phalangers.

E. G. BOULENGER, F.Z.S.

Description of a new Lizard of the Genus *Chalcides*, from the Gambia, living in the Society's Gardens.

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The following Papers have been received:—

IVOR G. S. MONTAGU, F.Z.S.

On a further Collection of Mammals from the Inner Hebrides.

F. R. WELLS.

On the Morphology and Development of the Chondocranium of the larval *Clupea harengus*.

R. I. POCKOCK, F.R.S., F.Z.S.

On the External Characters of the Beaver (Castoridae) and some Squirrels (Sciuridae).

ARTHUR LOVERIDGE, F.E.S., C.M.Z.S.

Notes on East African Birds (chiefly nesting-habits and stomach-contents) collected 1915-1919.

C. A. ADAIR DIGHTON, M.B., F.R.C.S., F.Z.S.

Coat-colour in Greyhounds.

EKENDRANATH GOSH, M.Sc., M.D., F.R.M.S., F.Z.S.

On the Animal of *Scaphula* Benson, with the Description of a new Species of *Scaphula*.

J. H. LLOYD, M.Sc., F.Z.S., and EDITH M. SHEPPARD, B.Sc., F.Z.S.

A Contribution to the Anatomy of a Hammerhead-Shark (*Zygæna malleus*).

E. LEONARD GILL, M.Sc.

The Permian Fishes of the Genus *Acentrophorus*.

R. H. MEHRA, M.Sc.

Two new Indian Species of the little-known Genus *Aulodrilus* (Bretscher), aquatic Oligochaeta belonging to the Family Tubificidae.

CHARLES F. SONNTAG, M.D., F.Z.S.

On the Vagus and Sympathetic Nerves of the Terrestrial Carnivora.

E. A. STENSIÖ.

Notes on certain Crossopterygians.

M. L. BHATTIA, M.Sc., F.R.M.S.

The Nervous System of *Scolopendra morsitans* Buffon.

J. STEPHENSON, M.B., D.Sc., F.Z.S.

The Oligochaeta of the Oxford University Spitsbergen Expedition.

GOBIND SINGH THAPAR, M.Sc.

On the Arterial System of the Lizard *Varanus bengalensis* Daud., with Notes on *Uromastix* and *Hemidactylus*.

W. E. H. HODSON, F.Z.S.

A Comparison of (A) the External Morphology of the Mouth-parts and (B) the Internal Morphology and Degree of Development of the Silk Press in typical Lepidopterous and Tenthredinid (Hymenopterous) Larvæ.

EDWARD PHELPS ALLIS, Jr., F.R.M.S., F.Z.S.

The Postorbital Articulation of the Palato-quadrate with the Neurocranium in the Cœlacanthidæ.

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The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

*October 31st, 1922.*



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

November 7th, 1922.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,  
in the Chair.

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Prof. G. ELLIOT SMITH, M.D., F.R.S., F.Z.S., exhibited, and made remarks upon, a series of photographs of a fossil tooth (*Hesperopithecus*) from Nebraska.

Dr. A. SMITH WOODWARD, F.R.S., F.Z.S., exhibited, and made remarks upon, drawings and photographs comparing teeth of a Bear, Chimpanzee, and *Hesperopithecus*.

Mr. C. S. ELTON communicated his paper "On the Colours of Water-Mites."

Prof. E. B. POULTON, M.A., F.R.S., F.Z.S., gave an account, illustrated with lantern-slides, of a series of experiments conducted at the Laboratory of the Marine Biological Association, Plymouth, in 1890, demonstrating that Commensalism may be beneficial to Crustacea.

Dr. G. M. VEVERS, M.R.C.S., L.R.C.P., F.Z.S., gave a *résumé* of his paper on "Nematode Parasites of Mammals from the Zoological Society."

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The following papers were taken as read:—W. J. KAYE, F.E.S., "New Species of Trinidad Moths"; CHAS. F. SONNTAG, M.D., F.Z.S., "On the Myology and Classification of the Wombat, Koala, and Phalangers"; E. G. BOULENGER, F.Z.S., "Description of a new Lizard of the Genus *Chalcides*, from the Gambia living in the Society's Gardens."

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The next Meeting of the Society for Scientific Business will be held on Tuesday, November 21st, 1922, at 5.30 P.M., when the following communications will be made:—

The SECRETARY.

Report on the Additions to the Society's Menagerie during the month of October, 1922.

IVOR G. S. MONTAGU, F.Z.S.

On a further Collection of Mammals from the Inner Hebrides.

F. R. WELLS.

On the Morphology and Development of the Chondocranium of the larval *Clupea harengus*.

R. I. POOCK, F.R.S., F.Z.S.

On the External Characters of the Beaver (*Castoridæ*) and some Squirrels (*Sciuridæ*).

ARTHUR LOVERIDGE, F.E.S., C.M.Z.S.

Notes on East African Birds (chiefly nesting-habits and stomach-contents) collected 1915-1919.

E. A. STENSIÖ.

Notes on certain Crossopterygians.

EKENDRANATH GHOSH, M.Sc., M.D., F.R.M.S., F.Z.S.

On the Animal of *Scaphula* Benson, with the Description of a new Species of *Scaphula*.

J. H. LLOYD, M.Sc., F.Z.S., and EDITH M. SHEPPARD, B.Sc., F.Z.S.

A Contribution to the Anatomy of a Hammerhead-Shark  
(*Zygæna malleus*).

R. H. MEHRA, M.Sc.

Two new Indian Species of the little-known Genus *Aulodrilus* (Bretscher), aquatic Oligochæta belonging to the Family Tubificidæ.

J. STEPHENSON, M.B., D.Sc., F.Z.S.

The Oligochæta of the Oxford University Spitsbergen Expedition.

R. J. ORTLEPP, M.A.

The Nematode Genus *Physaloptera*, Rud.

G. M. VEVERS, M.R.C.S., L.R.C.P., F.Z.S.

On the Cestode Parasites from Mammalian Hosts which died in the Gardens of the Zoological Society of London, during the Years 1919-1921; with a Description of a new Species of *Cyclorchida*.

The following Papers have been received :—

C. A. ADAIR DIGHTON, M.B., F.R.C.S., F.Z.S.

Coat-colour in Greyhounds.

E. LEONARD GILL, M.Sc.

The Permian Fishes of the Genus *Acentrophorus*.

CHARLES F. SONNTAG, M.D., F.Z.S.

On the Vagus and Sympathetic Nerves of the Terrestrial Carnivora.

EDWARD PHELPS ALLIS, Jr., F.R.M.S., F.Z.S.

The Postorbital Articulation of the Palato-quadrates with the Neurocranium in the Cœlacanthidæ.

A. J. HESSE, B.Sc., Ph.D.

A Description of Two new *Cercariæ* from *Limnæa peregra*, Muller.

GEORGE S. GIGLIOLI, M.D.

On the Linguatulid Arachnid, *Raillietiella furcocerca* (Diesing, 1835), Sambon, 1922.

RITA MARKBREITER, B.Sc.

Some *Microfilaria* found in the Blood of Birds dying in the Zoological Gardens, 1920-1921.

A. J. HESSE, B.Sc., Ph.D.

A Description of a new Nematode of the Genus *Capillaria* from the Minnow.

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The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,  
*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,  
REGENT'S PARK, LONDON, N.W. 8.  
November 14th, 1922.

ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

November 21st, 1922.

Sir S. F. HARMER, K.B.E., F.R.S., Vice-President,  
in the Chair.

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The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of October, 1922.

Prof. E. W. MACBRIDE, F.R.S., F.Z.S., exhibited, and made remarks upon, a series of lantern-slides bearing upon Dr. Kammerer's experiments on Amphibia.

Dr. A. SMITH WOODWARD, F.R.S., F.Z.S., exhibited, and made remarks upon, a skull and tusks of a Mammoth from Siberia, and drew attention to the remarkably perfect and fresh condition of the specimen.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, the shed lining of the gizzard of a Hornbill.

The Hon. IYOR G. S. MONTAGU, F.Z.S., communicated his paper "On a further Collection of Mammals from the Inner Hebrides."

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\* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.



Mr. F. R. WELLS gave a *résumé* of his paper on "The Morphology and Development of the Chondrocranium of the Larval *Clupia harengus*."

Mr. R. I. Pocock, F.R.S., F.Z.S., communicated his paper on "The External Characters of the Beaver (*Castoridæ*) and some Squirrels (*Sciuridæ*)."

Dr. G. M. VEVERS, M.R.C.S., L.R.C.P., F.Z.S., gave a *résumé* of his paper "On the Cestode Parasites from Mammalian Hosts which died in the Gardens of the Zoological Society of London, during the Years 1919-1921; with a Description of a new Species of *Cyclorchida*."

The following communications were taken as read:—ARTHUR LOVERIDGE, F.E.S., C.M.Z.S., "Notes on East African Birds (chiefly nesting-habits and stomach-contents) collected 1915-1919; E. A. STENSIÖ, "Notes on certain Crossopterygians"; EKENDRANATH GHOSH, M.Sc, M.D., F.R.M.S., F.Z.S., "On the Animal of *Scaphula* Benson, with a Description of a new Species of *Scaphula*"; J. H. LLOYD, M.Sc., F.Z.S., and EDITH M. SHEPPARD, B.Sc., F.Z.S., "A Contribution to the Anatomy of a Hammerhead-Shark (*Zygæna malleus*)"; R. H. MEHRA, M.Sc., "Two new Indian Species of the little-known Genus *Aulodrilus* (Bretscher), aquatic Oligochæta belonging to the Family Tubificidæ"; J. STEPHENSON, M.B., D.Sc., F.Z.S., "The Oligochæta of the Oxford University Spitsbergen Expedition"; R. J. ORTLEPP, M.A., The Nematode Genus *Physaloptera*, Rud."

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The next Meeting of the Society for Scientific Business will be held on Tuesday, February 6th, 1922, at 5.30 P.M.

A notice stating the Agenda for the Meeting will be circulated early in January.

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The following Papers have been received:—

C. A. ADAIR DIGHTON, M.B., F.R.C.S., F.Z.S.

Coat-colour in Greyhounds.

E. LEONARD GILL, M.Sc.

The Permian Fishes of the Genus *Acentrophorus*.

CHARLES F. SONNTAG, M.D., F.Z.S.

On the Vagus and Sympathetic Nerves of the Terrestrial Carnivora.

EDWARD PHELPS ALLIS, Jr. F.R.M.S., F.Z.S.

The Postorbital Articulation of the Palato-quadrates with the Neurocranium in the Cœlacanthidæ.

GEORGE S. GIGLIOLI, M.D.

On the Linguatulid Arachnid, *Raillietiella furcocerca* (Diesing, 1835), Sambon, 1922.

RITA MARKBREITER, B.Sc.

Some *Microfilaria* found in the Blood of Birds dying in the Zoological Gardens, 1920-1922.

Prof. EINAR LÖNNBERG, F.M.Z.S.

Remarks on some Palearctic Bears.

E. W. SHANN, B.Sc., F.Z.S.

The Embryonic Development of the Porbeagle-Shark, *Lamna cornubica*.

ROBERT GURNEY, M.A., F.Z.S.

Some Notes on *Leander longirostris*, M.-Edwards, and other British Prawns.

T. H. RING.

The Elephant-Seals of Kerguelen Land.

CHAS. F. SONNTAG, M.D., F.Z.S.

The Comparative Anatomy of Tongues of the Mammalia.—VIII. Carnivora.

ARTHUR LOVERIDGE, F.E.S., C.M.Z.S.

A List of the Lizards of British East Africa (Uganda, Kenya Colony, Tanganyika Territory, and Zanzibar) with Keys for the Diagnosis of the Species.

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The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

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Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,  
REGENT'S PARK, LONDON, N.W. 8.  
*November 28th, 1922.*

# ZOOLOGICAL SOCIETY OF LONDON.

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THIS Society was founded in 1826 by Sir STAMFORD RAFFLES, Mr. J. SABINE, Mr. N. A. VIGORS, and other eminent Naturalists, for the advancement of Zoology and Animal Physiology, and for the introduction of new and curious subjects of the Animal Kingdom, and was incorporated by Royal Charter in 1829.

---

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The Society consists of Fellows, and Honorary, Foreign, and Corresponding Members, elected according to the By-Laws. It carries out the objects of its foundation by means of its collection of living animals, by its Library, and by its Scientific Publications.

The Office of the Society, Regent's Park, N.W.8, where all communications should be sent, addressed to "The Secretary," is open from Ten till Five, except on Saturdays, when it closes at ONE P.M.

The Library, under the superintendence of Mr. F. Martin Duncan, F.Z.S., F.R.M.S. is open daily (except Sunday) from Ten A.M. till Five P.M.; on Saturdays, Ten A.M. till One P.M.

The Library is closed from Good Friday to Easter Monday, and upon all other Bank Holidays. It is also closed annually for cleaning purposes during the whole month of September.

The Meetings of the Society for General Business are held in the Meeting Room at the Society's Office on the third Wednesday of the month at 4.30 P.M. except in September and October.

The Meetings for Scientific Business are held in the Meeting Room at the Society's Office fortnightly on Tuesdays, except in July, August, September, and December and January, at half-past Five o'clock P.M.

The Anniversary Meeting is held on the 29th of April, or the nearest convenient day, at Four P.M.

The Society's Gardens are open daily from Nine o'clock until Sunset. Mr. R. I. Pocock, F.R.S., F.L.S., is the resident Superintendent and Curator of Mammals, Mr. D. Seth-Smith is Curator of Birds and Inspector of Works, Mr. E. G. Boulenger is Curator of Reptiles, Miss L. E. Cheesman, F.E.S., is Curator of Insects. Applications for anatomical material or facilities for work in the Prosectorium should be addressed to the Secretary.

### TERMS FOR THE ADMISSION OF FELLOWS.

FELLOWS pay an Admission Fee of £5, and an Annual Contribution of £3, due on the 1st of January, and payable in advance, or a Composition of £45 in lieu thereof; the whole payment, including the Admission Fee, being £50.

No person can become a FELLOW until the Admission Fee and first Annual Subscription have been paid, or the annual payments have been compounded for.

FELLOWS elected in November and December are not liable for the Subscription for the year in which they are elected.



## PRIVILEGES OF FELLOWS.

FELLOWS have Personal Admission to the Gardens upon signing their names in the book at the entrance gate, and may introduce Two Companions daily.

The WIFE or HUSBAND of a FELLOW can exercise these privileges in the absence of the Fellow.

Until further notice, FELLOWS will receive 40 undated Green Cards, available on any Sunday or week-day up to the end of February of the year following the year of issue, and 20 White Cards available on any week-day up to the same date. Twenty of the Green Cards may be exchanged for a book containing two Orders for each Sunday in the year. Twenty White Cards may be exchanged for a book of dated Week-day Orders, each Order available for any day during the week except Sunday. Special children's tickets are no longer issued, but the Green and White Cards are perforated, and each half is valid for a Child under twelve years of age. It is particularly requested that Fellows *will sign every ticket* before it goes out of their possession. Unsigned tickets are not valid.

FELLOWS are not allowed to pass in friends on their written order or on presentation of their visiting cards.

FELLOWS have the privilege of receiving the Society's ordinary Publications issued during the year upon payment of the additional Subscription of One Guinea. This Subscription is due upon the 1st of January, and must be paid before the day of the Anniversary Meeting, after which the privilege lapses. FELLOWS are likewise entitled to purchase these Publications at 20 per cent. less than the price charged to the public. A further reduction of 20 per cent. is also made upon all purchases of Publications issued prior to 1881, if above the value of Five Pounds.

FELLOWS also have the privilege of subscribing to the Annual Volume of 'The Zoological Record,' which gives a list of the Works and Publications relating to Zoology in each year, for the sum of Two Pounds Ten Shillings. Separate divisions of volumes 39 onwards can also be supplied. Full particulars of these publications can be had on application to the Secretary.

FELLOWS may obtain a TRANSFERABLE IVORY TICKET admitting two persons, available throughout the whole period of Fellowship, on payment of Ten Pounds in one sum. A second similar ticket may be obtained on payment of a further sum of Twenty Pounds.

Any FELLOW who intends to be absent from the United Kingdom during the space of at least one year, may, upon giving to the Secretary notice in *writing*, have his or her name placed upon the "dormant list," and will then be called upon to pay an annual subscription of £1 only during such absence, or in the event of returning to the United Kingdom before June 30th in any year to pay the balance of the ordinary subscription. After three years a Dormant Fellow must make a further application to be retained on that list.

Any FELLOW, having paid all fees due to the Society, is at liberty to withdraw his or her name upon giving notice in *writing* to the Secretary.

Ladies or Gentlemen wishing to become Fellows of the Society are requested to communicate with "The Secretary."

P. CHALMERS MITCHELL,

*Secretary.*

Regent's Park, London, N.W. 8.

January, 1923.

## MEETINGS

OF THE

## ZOOLOGICAL SOCIETY OF LONDON

FOR

## SCIENTIFIC BUSINESS.

1923.

TUESDAY, FEBRUARY	.....	6 and 20.
„ MARCH	.....	6 „ 20.
„ APRIL	.....	10 „ 24.
„ MAY	.....	8 „ 21.
„ JUNE	.....	12.

*The Chair will be taken at half-past Five o'clock precisely.*

# ZOOLOGICAL SOCIETY OF LONDON.

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## LIST OF PUBLICATIONS.

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THE scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are issued in the volumes of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described therein. Amongst such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, paged consecutively, during the months of March, June, September, and December. From January 1901 they have been issued as two half-yearly volumes, indexed separately.

An "Abstract of the Proceedings" is published by the Society on the Tuesday following the date of the Scientific Meeting to which it refers. It is issued along with the "Proceedings," free of extra charge, to all Fellows who subscribe to the Publications, but it may be obtained on the day of publication at the price of Sixpence, or, if desired, sent post free for the sum of Six Shillings per annum, payable in advance.

The "Transactions" contain such of the communications made to the Scientific Meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of One Guinea *before* the day of the Anniversary Meeting, are entitled to receive the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 20 per cent. less than the price charged to the Public. A further reduction of 20 per cent. is made upon purchases of Publications issued prior to 1881, if they exceed the value of Five Pounds.

Fellows also have the privilege of subscribing to the Zoological Record for a sum of Two Pounds Ten Shillings (which includes cost of delivery), payable on the 1st of July in each year; but this privilege is forfeited unless the subscription be paid *before* the 1st of December following.

The following is a complete list of the publications of the Society already issued.

# TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

4to. 20 vols. and Index.				Price to Fellows.				Price to the Public.			
Vols. I.-IV. (out of print).											
Vol.	V., containing 67	Plates ..	(1862-66) ....	5	4	3	....	6	19	0	
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	(June 1916) .....			2	5	0	....	3	0	0	

Since 1916 (Vol. XXI. Part I.) publication of the Society's Transactions has been temporarily suspended, owing to the high cost of production.

In consequence of a re-arrangement of the stock of the 'Transactions,' the Society is now able to offer for sale, at the reduced price of £30, sets of Vols. V.-XVI. inclusive, and separate papers, of which a list can be supplied, at about one-fourth their published price.

## PROCEEDINGS OF THE COMMITTEE OF SCIENCE AND CORRESPONDENCE OF THE ZOOLOGICAL SOCIETY OF LONDON. 8vo. 2 vols. (Letterpress only).

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the Grounds; (3) a short description of some of the principal  
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**ZOOLOGICAL RECORD**.—Vol. 57, containing literature relating  
chiefly to the year 1920, was published in August 1922,  
price £2. Vol. 58, for the year 1921, is being prepared as  
usual, price £3, or subscription, if paid in advance, £2 10s. 0d.

P. CHALMERS MITCHELL,

*Secretary.*

Regent's Park, London, N.W. 8.  
January, 1923.

*These publications may be obtained at the SOCIETY'S OFFICE  
or through any bookseller.*

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## NOTICE.

The 'Proceedings' for the year are issued in *four* parts, paged consecutively, so that the complete reference is now P. Z. S. 1922, p. . . . The Distribution is usually as follows:—

Part	I.	issued in March.
"	II.	" June.
"	III.	" September.
"	IV.	" December.

'Proceedings,' 1922, Part III. (pp. 483-835), was published on September 28th, 1922.

The Abstracts of the 'Proceedings,' Nos. 232-234, are contained in this Part.

The dates of Publication of 'Proceedings' 1830-1858 will be found in the 'Proceedings' for 1893, page 436.

The dates of Publication of 'Transactions' 1833-1869 will be found in the 'Proceedings' for 1913, page 814.

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